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VOL. 32, NO. 1 March, 1957

THE QUARTERLY REVIEW *of* BIOLOGY

SYMPOSIUM ON THE EFFECTS OF IONIZING RADIATION ON PLANTS

INTRODUCTORY REMARKS

By ARNOLD H. SPARROW

Biology Department, Brookhaven National Laboratory

CONSIDERING the overall interest in the field of radiobiology, a symposium dealing with the general topic of the effects of ionizing radiation on plants is perhaps overdue. It thus seemed particularly appropriate to hold such a symposium at the 1956 meeting of the AIBS, since this is both the fiftieth anniversary of the Botanical Society of America and the sixtieth anniversary of the first botanical experiments utilizing x-rays.

Within a year after the announcement of the discovery of x-rays by Roentgen in December 1895 papers began to appear describing injurious effects of x-radiation on plants. The discovery of natural radioactivity by Becquerel in 1896 also gave further impetus to investigations concerning the biological effects of ionizing radiations, and it is interesting to note that a book of 278 pages pertaining to the effects of ionizing radiation on plants was published by Gager as early as 1908. After the first decade of radiobiology there was sporadic but continued interest in the effects of ionizing radiations on plants. During the nineteen-twenties there was a rapid rise in number of publications and another period of rapid growth began about 1945. Fig. 1 illustrates the slow initial start and later rapid increases in numbers of publications in this field.

The relatively slow growth of radiobotany compared to radiobiology in general can perhaps be attributed to the lack of practical or useful applications. It also may be the result of a greater reluctance among botanists to explore a borderline field in which they had little experience or interest.

The first important upsurge of interest came

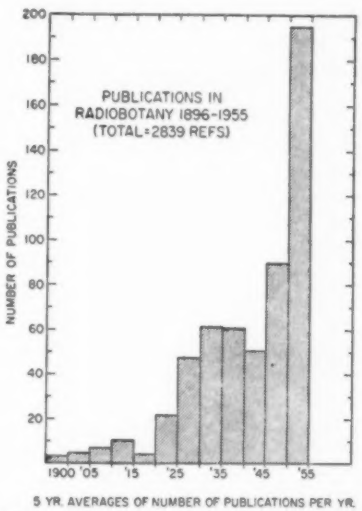

FIG. 1. AVERAGE NUMBER OF PUBLICATIONS IN RADIOLOGICAL BOTANY, 1896–1955, BY 5-YEAR AVERAGES

The data, pertaining to publications in radiobotany, are taken from a bibliography being assembled by the author relating to the effects of all kinds of ionizing radiation on plants or plant structures (not including papers relating to the use of radioisotopes as tracers).

shortly after the publications in 1927 of Muller and Stadler which showed that x-rays could speed up dramatically the frequency of mutations. This discovery, now supplemented by the demonstration that useful mutations can be induced in many plant species, has contributed much to the current strong interest in so-called "mutation breeding", i.e., the use of induced mutations in plant breeding. This interest has been heightened, of course, by the advent and general availability of artificial radioisotopes, and by the fact that during the last decade more funds have become available to support radiobiological research both in university and governmental laboratories.

By-products of the nuclear age, such as kilocurie sources of radiation or high intensity nuclear radiations in or near reactors, also have helped indirectly to stimulate experimental work on various plant materials, including large-scale field irradiations. During the last five or six years a whole new field of investigation pertaining to food processing and food storage has developed. Present indications are that within the next decade ionizing radiation may well come into commercial use along with the current methods of heat sterilization and cold storage as an alternative means of preservr ing various plant products.

Fortunately, fundamental research in radiobotany has been stimulated by these developments and important new knowledge has been gained also in biochemistry, physiology, and developmental anatomy. Much work remains to be done, however, before the primary mechanisms of radiation damage in plants can be understood. For instance, it is not definitely known for many effects whether the cytoplasm or the nucleus is the main site of the critical damage, and for many effects there is little or no clue as to the nature of the protoplasmic disturbance which leads to a given end result.

It is hoped that this symposium may help to stimulate further interest in radiobotany and that publication of the papers together in one issue of a journal will facilitate a review of the subject for those who wish to use it either in teaching or in research.

I. THE EFFECTS OF IONIZING RADIATION ON PLANTS: BIOCHEMICAL AND PHYSIOLOGICAL ASPECTS

By SOLON A. GORDON

Division of Biological and Medical Research, Argonne National Laboratory

THIS symposium is addressed to a group heterogeneous in respect to biological discipline. To my knowledge it is also the first symposium in the AIBS on the effects of ionizing radiation on plants. It seemed appropriate, therefore, to make this first paper a generalized discussion aimed primarily at the plant biologist and not the radiation biologist. First, I will speak briefly on what ionizing radiation is; second, on what is thought to happen when such radiation is absorbed by relatively simple systems; and finally, on how several biochemical and physiological responses of the irradiated plant might be associated.

Attracting the interest of the plant worker to these phenomena is more than an abstract consideration. For example, I recall the recent Radiation Research Society meetings at which there was a symposium on radiation effects in biological systems. It was readily apparent that little work had been done on biochemical responses of the plant to ionizing radiation, and not very much more on physiological effects. It might be pointed out, of course, that the study of plant responses to ionizing radiation is a relatively new field, and that biological disciplines generally begin at a gross descriptive level. Visible changes are nevertheless terminal manifestations of micro-events; the sequence of phenomena that occurs when the organism is exposed to high energy radiation may be represented as in Fig. 1. Initially there is a change at the submolecular level of organization. If this change is not reversed within a relatively short time, altered physico-chemical patterns ensue either directly, or via modification in genic structure or relationship. This, in turn, gives rise to physiological changes that find expression in a gamut from minor alterations in form to death—the inability to reproduce at any organizational level. Obviously, kingdom demarcations between the plant and animal tend to disappear in moving from right to left in the sequence. As was implied a moment ago, the major fraction of the work on plant responses to ionizing radiation has been with morphological changes at the cellular, tissue or organ level.

I have used interchangeably the terms "high energy" and "ionizing" radiation. What distinguishes this type of radiation from other types?

Radiation may be considered as the movement through space of energy, in either corpuscular or electromagnetic form. Corpuscular radiation consists of streams of atomic or sub-atomic particles that can transfer their kinetic energy to any matter with which they collide. The particles may be negatively charged, such as the electrons in beta rays, positively charged, as the helium nuclei of alpha rays, or electrically neutral, as the neutrons. The energy of the particle is largely determined by its velocity. Its interaction with matter depends principally upon the atomic structure of the matter. Electromagnetic radiation, on the other hand, may be thought of as a self-propagating stream of particles, called photons, that possess zero rest mass and no charge. It travels with a constant velocity, the velocity of light. In motion, however, it behaves as if it were a series of waves, with both electrical and magnetic components; its energy depends on the frequency of vibration of these waves. Radio waves, visible light, x- and γ-rays are fundamentally similar classes of electromagnetic radiation that are separated on the basis of their respectively increasing vibration frequencies.

According to the principle established by Grotthus, only radiation which is absorbed can be chemically active. When radiation is absorbed, the energy transfer seems to occur in discrete packets. The photon or quantum is the amount of energy capable of being transferred on absorption of one of these energy packets.

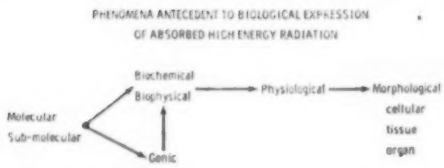

FIG. 1. PHENOMENA ANTECEDENT TO BIOLOGICAL EXPRESSION OF ABSORBED HIGH ENERGY RADIATION

What happens to a molecule "excited" by the absorption of a photon? The energy can be dissipated by motion or thermal vibration. Or the energy can be liberated by fluorescence—the emission of another photon lower in frequency. If the total energy is high enough, it may be dissipated, in part, by ejection of an electron from the absorbing atom or molecule. In other words, an ionization or separation of electron charges results. I mentioned a moment ago that as we go from radio waves to light to x-rays in the electromagnetic spectrum the vibration frequency rises. But as the frequency rises, the quantum energy rises proportionately according to the relation $E = h\nu$, where h is a constant and ν is the frequency. Ionizing radiation is simply that portion of the spectrum where the photon frequency is high enough so that photon absorption results in a charge separation in the absorbing entity, generally by electron ejection.

A certain minimum amount of energy is required to overcome the force binding an electron to an atom or one atom to another. The lower radiation frequencies, radio waves and visible light, are not able to knock out electrons from substances of biological interest. As we move to frequencies over 10^{17} cycles per second, we move into a succession of electron-emitting phenomena in the x-ray range. First the photon gives up virtually all of its energy to an atomic electron, which is then ejected. As the frequency rises, more and more photons rebound from collision with electrons as scattered radiation of lower energy; the energy lost is transferred to the electron thrown out by collision recoil. Very high frequency photons above 10^{21} cycles per second (energies above, roughly, 10^6 electron volts) can lose their energy in the creation of mass, the mass being eventually reconverted to quanta of x-radiation. Corpuscular radiation of sufficient energy also produces ionization. It may do so directly by displacement of shell electrons, or by knocking out a proton from an atom with which it collides. Or, it may produce ionization indirectly after capture by the nucleus of an atom; the nucleus in turn becomes radioactive and disintegrates to liberate β- or γ-rays.

Two aspects of ionizing radiation might be stressed here. First, the energy transferred to an atom is often much greater than that required to eject an electron. Part of the excess energy appears in the expelled electron, now energetic enough to ionize other atoms with which it collides and to produce secondary electrons. After thousands of collisions, the electron has lost velocity or energy and is captured. If the electron is captured by an atom, a chemically reactive ion is produced. A molecule capturing an electron is usually unstable, decomposing to give reactive fragments called free radicals. Most of the ionizations initiated by x-rays are produced by the powerful secondary ejected electrons. This explains how a single x-ray photon produces many ionizations.

Second, an energetic particle can transfer some of its energy in flight to nearby atoms or molecules without causing ionization. This is called excitation or activation, since the atoms or molecules are now in a more energetic state. Thus, the total energy absorbed per ionization, or per ion pair formed, is about 30–35 ev, though only about 15 ev are required to ionize water, for example. The surplus of 15–20 ev is dissipated in molecular excitation. This is a considerable amount of energy when we consider that about 5 ev are required to break most organic bonds. If this surplus energy is spatially concentrated (i.e., not spread over too many atoms), it may, in turn, cause radical formation. Or it may activate chemical reactions, whose activation energies range between 1–10 ev.

The absorption of ionizing radiation, then, initially causes excitation and the production of free radicals and ions. These ions are different in character from the ions produced by the dissociation of salts in that they contain an uneven number of electrons. The unpaired or odd electron makes a free radical extremely reactive. Radicals are short-lived because of this reactivity (10^{-9} to 10^{-6} seconds in condensed systems). They will react with each other to form a primary chemical bond where two electrons are paired, *viz.*,

$$H:\dot{O}\cdot + \cdot\dot{O}:H \rightarrow H:O:O:H \quad (H_2O_2)$$

Or they will tend to become stabilized by gaining or losing an electron, *viz.*,

$$H:\dot{O}\cdot + e \rightarrow H:\dot{O}: \quad (OH^-)$$

Complex organic radicals tend to have longer lives, since resonance reduces the reactivity of the odd electron by distributing it over the whole molecule.

Photons of ionizing radiation are powerful enough to be completely democratic in regard to the molecular species with which they interact. Since protoplasm is structurally a colloidal suspension that is roughly three-fourths water, it is usually assumed that a major part of the energy transferred to a biological system occurs via its water. It is also considered that the biological effects of ionizing radiation are caused, in part, by the activated water. Fig. 2 shows one version of what happens when water stops quanta of ionizing frequencies. It serves to illustrate quite adequately the process of ionization and radical formation.

Along the lines we have discussed, Fig. 2 indicates an electron ejected from a water molecule with which a high-energy photon has collided, resulting in the formation of a hydroxyl radical (a). After many collisions, the electron is finally captured to yield a hydrogen atom or radical (b). These two uncharged radicals (H· and OH·) are chemically very reactive. They are powerful oxidizing and reducing agents and can readily break carbon-carbon or carbon-nitrogen bonds. In addition, hydrogen atoms can also bring about oxidation by dehydrogenation.

Hydrogen and hydroxyl radicals are believed to be the primary products of irradiated water. The presence of dissolved oxygen, however, can lead to the formation of other highly oxidative entities: hydroperoxyl radicals and hydrogen peroxide. The hydroperoxyl radical may arise from the reaction of a hydrogen atom with O_2 (c), or via the well-known affinity of oxygen for electrons (d). Hydrogen peroxide, in turn, may be formed by the stabilization of two hydroperoxyl radicals (e), or through electron capture by the hydroperoxyl group to yield the anion of H_2O_2 (f).

From Fig. 2 one would anticipate that the biological effect of an ionization would be potentiated in the presence of dissolved oxygen. The simplest explanation of such an oxygen potentiation of biological effect, which has been observed (but cf. Alper, 1956), would be that a greater number of reactive oxidative species are formed per ionization. While this may frequently occur in relatively simple *in vitro* systems, it is also probable that metabolic patterns are altered *in vivo* with changes in oxygen partial pressure and that this may influence the degree of radiation response.

The number of ionizations or ion pairs formed in an irradiated system can be either directly measured or indirectly deduced. Hence the number of solute molecules changed or inactivated per ionization can be approximated for the system as an index of the radiation potency. This index is known as the ionic yield (M/N). The most common dose unit used by the biologist in measuring ionizing radiation is the *roentgen* (r). For our purpose the r may be considered as the amount of energy dissipated in 1 gram of tissue or water in the production of 1.8×10^{12} ion pairs. This is equivalent to the absorption of approximately 93 ergs/g. The *roentgen equivalent physical* (rep) is a unit that facilitates comparison of various types of radiation. One rep denotes the release of the same amount of energy in a medium as would 1 r of x-rays.

I have used water as an illustration for the formation of ion pairs and radicals. Fundamentally similar electron phenomena take place when a solute molecule collides with a high-energy photon or particle. This, incidentally, touches on a controversial issue in the field of radiation effects. Does the energy responsible for initiating a solute change come *indirectly* from activated water or free radicals in the medium? Or does the solute itself act as a *direct* target for an ionizing particle? To pose the problem somewhat differently in terms you will hear developed later, breakage of chromo-

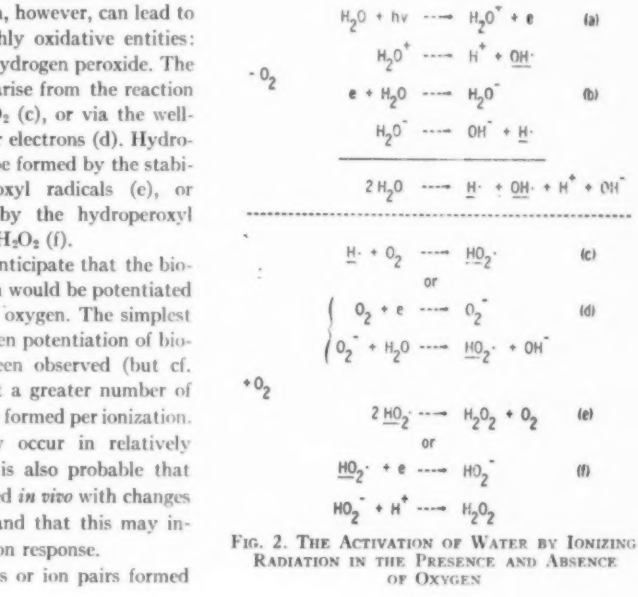
$H_2O + h\nu \longrightarrow H_2O^+ + e$ (a)
$H_2O^+ \longrightarrow H^+ + \underline{OH}\cdot$
$- O_2$
$e + H_2O \longrightarrow H_2O^-$ (b)
$H_2O^- \longrightarrow OH^- + \underline{H}\cdot$
$2\,H_2O \longrightarrow \underline{H}\cdot + \underline{OH}\cdot + H^+ + OH^-$
$\underline{H}\cdot + O_2 \longrightarrow \underline{HO_2}\cdot$ (c)
or
$O_2 + e \longrightarrow O_2^-$ (d)
$O_2^- + H_2O \longrightarrow \underline{HO_2}\cdot + OH^-$
$+ O_2$
$2\,\underline{HO_2}\cdot \longrightarrow H_2O_2 + O_2$ (e)
or
$\underline{HO_2}\cdot + e \longrightarrow HO_2^-$ (f)
$HO_2^- + H^+ \longrightarrow H_2O_2$

FIG. 2. THE ACTIVATION OF WATER BY IONIZING RADIATION IN THE PRESENCE AND ABSENCE OF OXYGEN

somes is a significant effect of low doses of radiation. The breakage might occur in the track where an ionizing particle crosses the chromosome. Or the break may be the site from which an electron is transferred to a hydroxyl radical that had been formed nearby in the medium. It should be considered, however, that the locus of damage may be the termination of a sequence of electron transfers traversing the macromolecule, a sequence initiated at a site other than the one where bond cleavage occurs.

As Dale (1954) has pointed out, the closer the origin of an active radical to the molecule or structure on which it acts, the less important becomes the distinction between direct and indirect action. Without developing the matter further here, the problem is one that bears on the ultimate mechanism of radiation damage. By and large, the indirect action theory is more flexible in regard to the distance between primary ionization and the site of damage. It is also more applicable for explaining in vitro radiochemical events in aqueous media.

With emphasis on the indirect action hypothesis, what happens to molecular species of biological interest when irradiated in an initially definable aqueous system? Suppose a solution of solute A is irradiated by x-rays at a constant rate to yield product B. B reacts with the radicals in the medium at a low rate compared to the reaction rate of A, and the rate of disappearance of A is not limited by its concentration. Then the number of molecules of A that are changed will be directly proportional to the radiation dose. The ionic yield will remain constant till the concentration of A becomes limiting. Such zero order inactivation curves are shown in the oxidation of ferrous to ferric ion (Fricke and Morse, 1929), the decomposition of formic acid (Fricke, Hart, and Smith, 1938), and the oxidation of cytochrome c (Guzman Barron and Bonzell, 1950) by x-radiation.

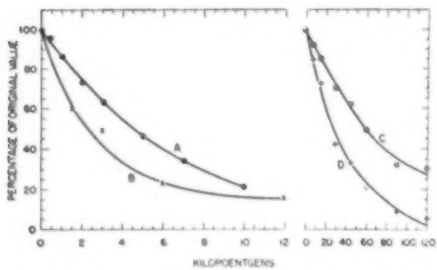

FIG. 3. EXPONENTIAL RELATION BETWEEN RESPONSE AND X-RAY DOSE IN SYSTEMS IN VITRO

Curve A, the decrease in concentration of the auxin indoleacetic acid (after Gordon and Weber, 1955). Curve B, the change in activity of carboxypeptidase against hydrolized edestin (after Dale, 1940). Curves C and D, the change in relative viscosities, corrected for the solvent, of nucleohistone and Na nucleate, respectively (after Sparrow and Rosenfeld, 1946).

TABLE 1

The concentration of various addends required for 50% protection of a 10^{-4} M solution of FAD against radiation damage (from Dale, 1942)

50% protection by:	
10^{-5} mol./ml.:	$10^{-7.5}$ mol./ml.:
Glycine	Glucose
Na oxalate	Sucrose
$NaNO_3$	KCNS
	Na formate
10^{-6} mol./ml.:	10^{-8} mol./ml.:
Leucylglycine	Fructose
Alanine	$NaNO_2$
$K_3Fe(CN)_6$	Na nucleate from yeast
$K_4Fe(CN)_6$	Na nucleate from thymus
10^{-7} mol./ml.:	
Na hippurate	

However, most organic molecular species yield irradiation products that are still capable of reacting with free radicals. The reaction products will "protect" the original solute. As the ratio of solute to product concentration decreases, the extent of protection increases and the solute concentration will decrease exponentially. Such exponential inactivation curves are observed on the irradiation of enzyme, auxin, and nucleoprotein solutions, as is illustrated in Fig. 3.

Obviously, co-solutes in an irradiated system may also compete for radicals and thus serve to decrease the rate of effect on the molecular species observed. Curves C and D in Fig. 3, for example, demonstrate the effect of protein in reducing the rate of viscosity change in DNA. Table 1, from the work of Dale (1942), further illustrates the phenomenon of protective effect. The table shows the concentration of various substances that will reduce by 50% the x-ray inactivation of a solution of alloxazine adenine dinucleotide, the prosthetic group of D-amino acid oxidase. Supplementing Fig. 3B, it indicates that nucleotides, as well as nitrite and fructose, are relatively effective protectants of the flavin dinucleotide. These studies, as well as many others in the literature, indicate quite clearly that the inactivation rate of a sub-

stance irradiated *in vitro* is modifiable by the relative amounts and reactivities of accompanying substances.

With primary interest in the *in vivo* inactivation of metabolic determinants, I will from here on emphasize work of our own laboratory on the effect of ionizing radiation on the phytohormone auxin (Gordon and Weber, 1955; Gordon, 1956a). Most biological compounds will be inactivated with ionic yields between, roughly, 10^{-2} and 10^{0} when irradiated as pure solutions. The auxin indoleacetic acid is not unique in this respect, being inactivated with ionic yields in the order of unity under a variety of conditions. It is protected by dilute plant extracts, plant proteins being rather effective in this respect. For example, auxin was irradiated with x-rays in the presence of Fraction I protein of spinach, the mass protein of the leaf cytoplasm. With the protein at $\frac{1}{100}$ the concentration of the auxin, the ionic yield for auxin inactivation was found to be $\frac{1}{100}$ that of auxin irradiated alone. On the basis of estimated collision frequencies for the auxin and protein molecules with water radicals, this reduction in ionic yield caused by the protein indicates that 10^{4} radicals were deactivated by the protein for every radical that was effective in auxin destruction.

But in plant tissues such as the leaf or coleoptile auxin occurs at concentrations in the order 10^{-10} to 10^{-11} g. moles/gram. It is surrounded by a heterogeneous mixture of potentially protective solutes. Proteins alone, if considered as discrete molecular units, are in 10^{3} to 10^{4} mole excess. It thus appears highly improbable that low doses of ionizing radiation will directly inactivate auxin or any other multimolecular cellular solute to any appreciable degree. Several instances of the numerous experimental works tending to support this generalization may be cited. Guzman Barron (1954) and coworkers in particular have shown that the thiol group of both simple sulfhydryl compounds and sulfhydryl enzymes in pure solution is readily inactivated by x-radiation. The ionic yields were between 4 and 0.1. Yet we could find no decrease in the sulfhydryl titer (using the nitroprusside test) of *Avena* embryos immediately subsequent to an irradiation of 4×10^{4} r of x-rays. The same dose, though eventually lethal, did not inhibit succinoxidase activity in young *Avena* germinants. Similarly, in animals, a number of sulfhydryl enzymes do not decrease in activity following exposure to lethal doses of x-rays. An unchanged gross sulfhydryl concentration is not necessarily inconsistent with the inactivation of specific thiol groups essential to cellular function. There appears to be no evidence, however, that this happens *in vivo* as a direct radiation effect. In regard to non-thiol enzymes, Table 2 dramatically illustrates the relative insensitivity of two oxidative systems in the potato tuber. It took 50 kr of x-radiation to show an effect on the cytochrome oxidase, whereas this enzyme was unaffected by 3×10^{6} r of γ-radiation. It took the latter dose of gamma radiation to decrease tyrosinase activity by 50 percent.

In contrast, x-ray dosages of less than 100 r reduce, within minutes, the concentration of auxin in plants. The phenomenon was first observed by Skoog (1935). Since then numerous responses of plants to ionizing radiation have been attributed to destruction of the growth hormone. The reduction in auxin level following x-irradiation of young green plants is indicated in Fig. 4. Yet, as we indicated in discussing the concentration of auxin in plant tissues, appreciable auxin photolysis in vivo by the lower range of doses shown in Fig. 4 is theoretically implausible. Though this order of dose is sufficient to induce cellular damage, the actual energy absorbed is small. It is only enough to cause direct chemical change of several hundred molecules per μ^3 of tissue. This is virtually the concentration of the free growth hormone alone.

We are thus led almost inescapably to the following two possibilities: (1) the energy absorbed by the plant tissues is dissipated preferentially in auxin destruction; or (2) the energy absorbed inactivates molecules or molecular relationships that are responsible for the turnover of many auxin molecules. If so, there must be a mechanism that

TABLE 2

Cytochrome oxidase and tyrosinase activity of potato tubers following x- and γ-irradiation
(from Sussman, 1953)

Dosage	Type of Radiation	Cytochrome Oxidase Activity	Tyrosinase Activity
(r)		*mm³ O_2/30 minutes*	*mm³ O_2/30 minutes*
Control	—	119, 108	225
40,000	γ-rays	114, 117	220, 200
400,000	γ-rays	100	200
3,200,000	γ-rays	122	90, 110
50,000	x-rays	94	212

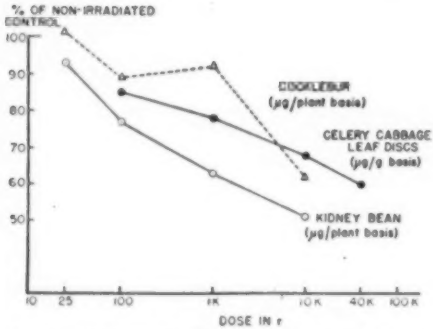

FIG. 4. CHANGES IN FREE AUXIN LEVEL IMMEDIATELY FOLLOWING X-IRRADIATION OF WHOLE PLANT SHOOTS OR SHOOT SEGMENTS

in effect "potentiates" or "multiplies" the energy originally absorbed. The decrease in auxin concentration would thus be an indirect result of a more primary radiation event. We were able to assess the probabilities of these alternatives by an experiment designed to evaluate the magnitude of direct destruction of the auxin in tissues.

Subapical tissues of the *Avena* coleoptile grow only by cellular elongation during the second and third day of germination. They require auxin for this growth, but cannot synthesize it. Growth in length of these tissues bears a proportional relation both to the auxin concentration supplied and to the amount of auxin which is destroyed during the growth process. An equivalence between growth and auxin destroyed can therefore be made. This equivalence was determined experimentally, and indicates that 5.2×10^{-13} moles of auxin disappear per mm. of elongation.

Suppose, then, coleoptile tissues are elongating under the influence of auxin. They are then irradiated. If auxin is destroyed by irradiation, the growth of the tissues will decrease proportionally to the amount of auxin inactivated. The coleoptile thus gives us a sensitive device for detecting auxin destruction *in vivo*. With estimates of the amount of auxin destroyed, and the amount of energy absorbed by the tissues, the radiation potency or efficiency can be calculated. Essential to the validity of this approach is the assumption that the potential ability of the tissues to grow, and to respond to auxin, is unimpaired by the radiation dose employed.

Subapical coleoptile sections were therefore immersed briefly in a weak solution of indoleacetic acid to maintain their elongation. They were then x-irradiated in a moist atmosphere and placed in water. The growth in the subsequent 12 hours was compared with non-irradiated controls. We were unable to find any reduction in growth resulting from irradiation until dosages of over 10^4 r were given. Apparently the extension of coleoptile sections, i.e., cellular expansion per se, is relatively resistant to ionizing radiation. This conclusion is consistent with other studies using plant organs more heterogeneous in growth pattern than the coleoptile (cf. Quastler and Baer, 1950; Gray and Scholes, 1951). Furthermore, since growth is proportional to the concentration of auxin in the tissues, any auxin destruction in vivo by low or moderate radiation doses would have resulted in decreased growth. This did not occur. From this we may deduce that auxin in the tissues was not sensitive to x-radiation doses below 10^4 r.

Between dosages of 10^4 and 10^5 r, growth inhibition progressively increases. When the sections were placed in auxin solution rather than water following irradiation, over 10^5 r were required to inhibit the subsequent growth. Otherwise stated, growth inhibitions following irradiation between 10^4 and 10^5 r could be reversed completely by addition of auxin. These dosages thus have no apparent effect on the growth potential of the tissues or on their reactivity to auxin. Therefore, let us assume that the growth inhibition following irradiations in the dose range of 10^4 and 10^5 r results from auxin destruction. Within this dose range, decrease in growth in mm. may be equated to moles of auxin inactivated, using the equivalence indicated above. The amount of auxin destroyed at each irradiation may then be calculated. This was done, and the ionic yield was found to decrease exponentially as a function of dose (r) according to the following approximation:

$$M/N = 6.6 \times 10^{-18}\, e^{-.01\,(r-1.5\times 10^4)}$$

where

$$r \geq 1.5 \times 10^4$$

This equation indicates that where the growth inhibition may be interpreted as a result of auxin destruction, it initially takes 10^{17} ionizations to destroy one auxin molecule. Otherwise stated, the statistical probability of any auxin molecule being damaged *in vivo* by x-radiation is initially less than one chance in 100 quadrillion. As irradiation continues this probability *decreases*. It is evident that the efficiency of auxin destruction in these tissues

is of relatively low order, and it is very probable that auxin in the plant is neither radiosensitive nor preferentially inactivated.

We are led, then, to the second possibility whereby the effect of low dose irradiation on auxin destruction is accomplished by a multiplier mechanism. An obvious candidate for the role is an enzyme whose damage will affect the turnover of many auxin molecules. You will recall from Fig. 4 that low doses of radiation caused the auxin concentration to drop in shoots of the kidney bean and cocklebur plants, and in leaf discs of the celery cabbage. These organs have active systems for auxin metabolism. The growth hormone is being constantly synthesized in the young leaves and meristems. At the same time it is being depleted by growth and by both enzymatic and non-enzymatic systems for auxin inactivation. On the other hand, subapical tissues of the coleoptile, where radiation does not decrease the auxin concentration, are unable to synthesize auxin and possess lower auxin depletion rates. These considerations suggested the following hypothesis to explain the effect of radiation on auxin economy. Though we know nothing of the kinetics of auxin metabolism in the plant, let us assume that the free growth hormone is a dynamic pool maintained as a steady-state system by concomitant biosynthetic and depletion reactions. If biosynthesis was preferentially and immediately radiosensitive, the rate of auxin formation would be decreased by, and during, irradiation. The level of the free auxin pool would drop, the magnitude and rapidity of the decrease being a function of the turnover rate of auxin. Conversely, the same result would ensue if the rate of auxin depletion was preferentially accelerated by irradiation. Therefore, the effect of x-rays on the biosynthesis and depletion of auxin was determined.

Young kidney bean plants, their roots shielded, were irradiated with x-rays. At various times after irradiation the free auxin level in the whole shoot was measured. The effects of various radiation doses are shown in Fig. 5. Doses between 25 r and 1 kr not only lowered the free auxin concentrations immediately following irradiation, but also depressed the auxin levels during the week following. With such doses a return to control level is attained in about two weeks. Recovery does not take place in this period, or subsequently, with the two highest dosages. Similar results to these were obtained when cocklebur plants were used.

We believe that such depressions of the free auxin level following x-irradiation of the plant are caused by a rapid curtailment of auxin biosynthesis rather than an accelerated auxin catabolism. This interpretation is based on a number of experimental studies that I will summarize.

1. We have not observed any manifestation of enhanced hormonal function and hence presumably increased rates of auxin utilization following irradiation. Where the radiation dose was large enough to have any effect, only inhibition was found in the elongation of *Avena* coleoptiles, in internode extension of *Phaseolus* stems, and in rooting of leafed *Populus* cuttings following irradiation, in each instance, of the total organ.

2. Auxin was added to breis made from irradiated and non-irradiated coleoptiles and *Xanthium* shoots. The breis were incubated both in the light and dark. Thus the effect of x-radiation on both photoinactivation as well as enzymatic and non-enzymatic auxin destruction could be estimated. In no experiment could we find any significant effect of irradiation on the amount of auxin recovered. In short, we could find no acceleration of any direct auxin depletion mechanism of the plant by x-radiation.

3. Growth of axillary buds is inhibited by the terminal bud of the shoot. The inhibition is caused by the auxin produced in and transported from

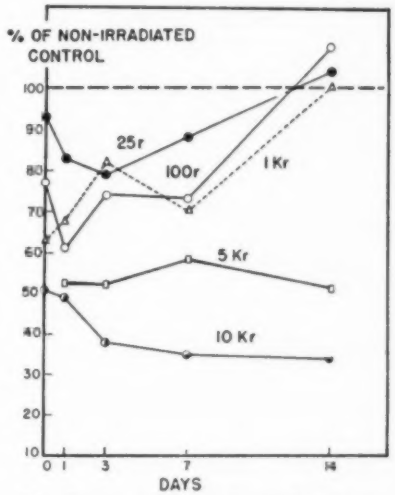

FIG. 5. RELATIVE FREE AUXIN LEVELS IN THE KIDNEY BEAN PLANT FOLLOWING X-IRRADIATION

the terminal bud. If the terminal bud is cut off (or severely injured) the axillary buds develop. If a decapitated bud is replaced by an exogenous source of auxin, the growth of the axillary buds remains suppressed. An appreciable inhibition of auxin synthesis in the apical bud should result, therefore, in the growth of axillary buds.

The terminal bud of the cocklebur plant was irradiated with 200 r of x-rays, the remainder of the plant being shielded with lead. Subjacent axillary buds began enlarging. They grew continuously for the subsequent month, virtually no growth taking place in the axillary buds of non-irradiated plants. If auxin was supplied to the irradiated terminal bud by external application for only two days following irradiation, axillary bud growth was simply postponed for two days. They then duplicated the growth response of the buds on irradiated but not auxin-treated plants. If, however, auxin was supplied for 2 weeks following irradiation, the axillary buds which had been kept suppressed remained dormant, though they had not lost their ability to grow. It is clear, then, that auxin was able to reverse the effect of the x-rays on the terminal bud as measured by the response of organs normally kept dormant by auxin formation in that bud. The temporal pattern of inhibition of terminal bud effect on the axillaries at two days and recovery in 2 weeks is consistent with the pattern of decrease and recovery in free auxin levels exhibited in Fig. 5. These results offer a less equivocal substantiation of the radiation sensitivity of auxin formation.

4. Consistent with this interpretation are the auxin reversals of the growth inhibition following irradiation of crown-gall tumor cells. Auxin is apparently required for the cellular duplication that comprises most of the tumor growth, as well as for the initial transformation of normal cells. The crown-gall contains an active system for auxin biosynthesis and can convert tryptophan to auxin with relative efficiency. Klein and Vogel (1956) inoculated tomato plants at the second node with crown-gall bacteria and permitted carcinogenic transformation to take place. The plants were then irradiated with neutrons, x- and γ-rays. Following irradiation, the apical node was removed and either lanolin or lanolin-containing indoleacetic acid was applied above the inoculation site. Table 3 shows the inhibition of subsequent tumor growth by both the corpuscular and electromagnetic radiation, and the ability of auxin to reverse the radiation effect of the dosages below 5 kr.

TABLE 3

Inhibition of the duplication of crown-gall tumor cells in vivo by ionizing radiation and reversal of inhibition with indoleacetic acid (from Klein and Vogel, 1956)

Radiation	Dose r or rep/min	Total Dose	Av. Tumor Diameter as % of Control	
			Lanolin	Lanolin IAA
Fast neutrons	3.4	340 rep	95	103
	3.4	550 rep	28	100
	4.6	950 rep	7	90
X-rays	10.6	500 r	99	100
	10.2	1000 r	76	98
	12.2	1500 r	8	80
	47.5	5000 r	7	7
Gamma rays	12.2	1500 r	106	106
	12.5	2100 r	58	101
	12.2	2850 r	7	90

5. The most compelling confirmation of the lability of auxin formation in the plant comes from direct biochemical examination of the plant itself. There is considerable ground for the assumptions that the native auxin of hormonal function in growth is indoleacetic acid, and that indoleacetic acid originates by the degradation of tryptophan (Gordon, 1956b). Though the biosynthetic pathway is uncertain, there is also presumptive evidence that the terminal stage of the sequence is the oxidation of indoleacetaldehyde to the acid. The effects of irradiation on these systems were examined.

Mung bean seedlings were irradiated with various doses of x-rays. Cell-free homogenates were made of each dose group within several minutes after irradiation. Each was assayed to determine the rate at which it could convert tryptophan to indoleacetic acid and indoleacetaldehyde. The results are represented in Fig. 6. They indicate that an x-ray dose as low as 10 r results in an 11% inhibition of the enzyme system, with the extent of inhibition dropping exponentially with increasing dose. There was no decrease in the amount of indoleacetaldehyde concomitantly formed. On the contrary, the precursor of the auxin appeared to increase in inverse proportion to the acid as the dose was raised. The apparent pileup of the aldehyde suggested that the radiation block occurred in the enzyme system that oxidizes the aldehyde to the acid. This was tested by determining the effect of x-rays on the ability of the homogenates to convert the aldehyde to the auxin (Fig. 7). The rate of inhibition shows the same order of sensi-

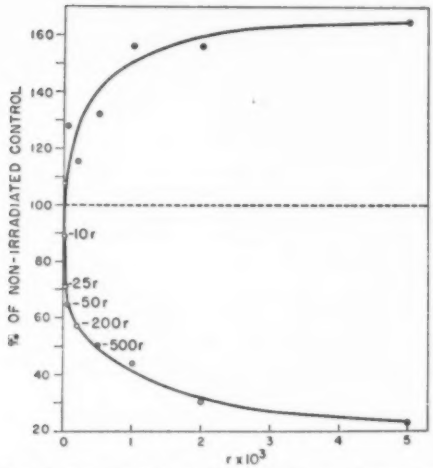

FIG. 6. CONVERSION OF TRYPTOPHAN TO AUXIN BY CELL-FREE HOMOGENATES OF X-IRRADIATED MUNG BEAN SEEDLINGS

The lower curve gives the relative amount of indoleacetic acid formed, the upper curve indoleacetaldehyde.

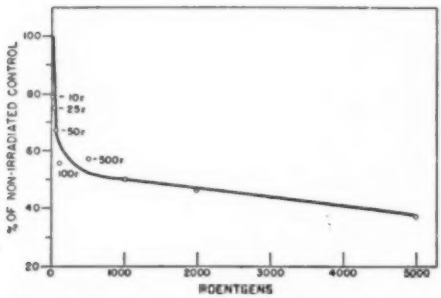

FIG. 7. CONVERSION OF INDOLEACETALDEHYDE TO INDOLEACETIC ACID BY CELL-FREE HOMOGENATES OF X-IRRADIATED MUNG BEAN SEEDLINGS

tivity and rapid diminution as does the total process of tryptophan conversion to auxin. It should be noted that 20 percent inhibition of the terminal enzyme in auxin formation resulted when the plant was irradiated with the dose of 10 r. Fig. 7 is explicit in its indication that the radiation damage occurs in the terminal stage of auxin biosynthesis.

In the preceding experiments the enzymatic damage was evaluated immediately subsequent to irradiation. What happens to the activity in the days following? The response of the auxin-forming system in the 2-week period after irradiation is given in Fig. 8. In these experiments tryptophan was infiltrated into the leaf and bud tissues of mung bean seedlings at each of the indicated times. The rate of auxin formation was then measured. Here again we have the same pattern of initial sensitivity and exponential decrease in extent of inhibition with increasing dose as shown both by the morphological studies and by the direct determinations of auxin levels. There is likewise the same pattern of recovery in biosynthetic ability: complete or virtually complete recovery in 1 to 2 weeks with doses below 1 kr, partial recovery with 2 kr and none at 5 kr. We thus have summarized three lines of experimental approach—physiological, morphological, and biochemical—that substantiate the relatively high sensitivity of auxin biosynthesis to ionizing radiation.

Might I emphasize that, in the biochemical experiments just described, enzyme activities were determined following irradiation of the plant. We are therefore dealing with an *in vivo* sensitivity. Secondly, enzymatic inhibition is detectable in preparations made within several minutes after irradiation. It may be inferred that cellular or nuclear replication is not required for expression of this radiation damage.

To clarify the latter inference, the intracellular distribution of the enzyme system was studied (Gordon, 1956c). It is found in the cells of young leaves and meristems as a non-particulate, soluble component of the cytoplasm. It is part of the complex "Fraction II" cytoplasmic proteins that fall between 0 and 4 Svedberg units in sedimentation velocity. This fraction constitutes practically all of the enzyme activities of the cytoplasm. With this knowledge, and with an approximation of the relation between radiation dose and the degree of inhibition, it is possible to estimate the number of

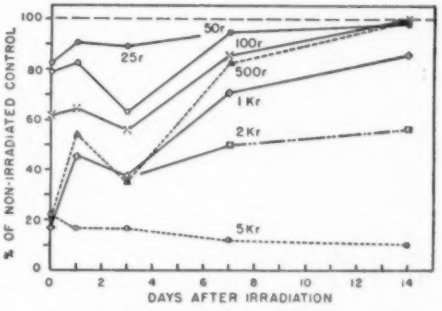

FIG. 8. CONVERSION OF INFILTRATED TRYPTOPHAN TO AUXIN BY MUNG BEAN SEEDLINGS AT VARIOUS TIMES AFTER IRRADIATION

enzyme molecules destroyed per ionization. When this is done, one obtains the amazing value of an ionic yield in the region of unity, plus or minus several orders of magnitude. This is equivalent to saying that the energy absorbed is to a large degree diverted to the inactivation of the auxin-forming enzyme, disregarding the molecular excess of other cellular species. In effect, these enzyme molecules appear as relatively enormous radiation targets. What we have done, then, is to arrive at the paradox previously introduced: how one extranuclear molecular species can be inactivated in a heterogeneous milieu of protective substances.

We might at this point repeat the whole of the preceding discussion at the next lower ontogenetic level. This would bring us again to an explanation founded on the dynamic aspects of cellular metabolism—specifically, that the auxin enzyme undergoes rapid turnover, and that the locus of radiosensitivity is an entity involved in either the formation or the depletion of the enzyme. Because of our complete lack of information on the nature and kinetics of these systems, all we have done again is to pinpoint the problem of apparent energy channelling to particular loci (cf. Pelc and Howard, 1952a).

If the primary target of the radiation damage was a conjugated molecular complex the size of the chromosome or gene, the problem would be somewhat simpler in relating the amount of energy absorbed to a specific biochemical impairment. The cytoplasmic analogue of the conjugated macromolecules of the nucleus would be organelles such as the mitochondrion. The study just described on intracellular localization of the enzyme demonstrated, however, that it is an extranuclear soluble component of the cytoplasm. Hence we may also infer that the site of primary damage is likewise in the cytoplasm. Gray (1954) has pointed out in this context that a significant property of a large structure, destroyable by a single particle, is continuity. If we consider the cytoplasm *in situ* not as discrete autonomous molecular units but rather as a bonded, continuous micellar net, we have our enormous radiation target. It is a target that permits not only intramolecular but also intermolecular electron transfer. Hence it is synonomous with a volume wherein energy flow may occur irrespective of whether its flow is initiated by a photon, secondary particle, or free radical. It may be suggested that electron ejection from any site in the net will start an electron migration to that site from labile, i.e., readily oxidizable or broken, bonds. The auxin-forming enzyme or its progenitor may be at such a locus. Or, alternatively, the disablement of a mechanism for electron transfer, a system essential to the function of the enzyme, may be the explanation for the enzymatic damage. We can only be vague as to how the enzyme is inactivated in this association. There is no reason to assume, *a priori*, that the indoleacetaldehyde-auxin enzyme is the only enzyme impaired by low or moderate doses of ionizing radiation. This point about the specificity of damage will serve very well to introduce the terminal portion of my discussion.

In dealing with radiation damage, we must differentiate between the immediate, primary effects and the changes that arise from disruption of key cellular or metabolic processes. It is frequently quite difficult to distinguish between the two. Two criteria might be the magnitude of the radiation dose involved, and the time lag between irradiation and response. In regard to the criterion of dose magnitude, we have no experimental basis for assuming a qualitative difference in the initial "targets" or damageable entities, though certainly qualitative differences in secondary responses are dose-dependent. Pragmatically, however, there are threshold levels of molecular disorganization which must be attained before a specific type of cellular damage is perceived. With this qualification in mind, how unique is the *in vivo* sensitivity of the auxin-synthesizing enzyme?

As far as I am aware, no biochemical sequence of the many so far examined, including protein and RNA synthesis (Pelc and Howard, 1952b), has shown an immediate sensitivity to low radiation doses other than DNA biogenesis. The sensitivity of DNA formation has been demonstrated by the radioautographic studies of Howard and Pelc (1953) on root cells of *Vicia faba*, and is backed by the more extensive isotopic work on animals (Bacq and Alexander, 1955), particularly the works of Hevesy and of Holmes. Though the inhibition of DNA synthesis can be picked up in the animal within an hour, the time of the first perceptible plant response has not been precisely established. It is probable that the inhibition also occurs very quickly after irradiation. Synthesis of DNA takes place during interphase in meristematic tissues. Cells that have been irradiated at this mitotic stage do not elaborate DNA and have their mitotic activity delayed. The degree of inhibition is roughly dose-dependent, the effect of 35 r being detectable.

It will be recalled that the inhibition of auxin

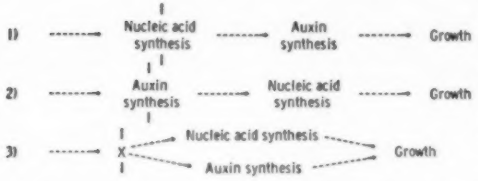

FIG. 9. POSSIBLE LOCI OF BIOCHEMICAL DAMAGE IN THE INHIBITION OF GROWTH BY IONIZING RADIATION

formation or tryptophan conversion tends to disappear within several days to two weeks, depending on the radiation dose, with no recovery above the dose range of 1 kr–2 kr (see Figs. 5 and 8). In oral discussion, L. H. Gray pointed out that this pattern of inhibition and recovery parallels almost identically the inhibition and recovery of mitotic activity in meristems. From the work of Howard and Pelc, it may be inferred that the inhibition of DNA synthesis causes the mitotic inhibition. Since both auxin and DNA are required for cellular replication, radiation damage to the growth of plant tissue may be related to auxin and DNA biogenesis in the relationships indicated by Fig. 9. These relationships postulate the not necessarily exclusive possibilities: 1) that DNA is required for and is synthesized sequentially previous to auxin formation, the radiation block occurring in the formation of the nucleic acid; 2) that the primary radiation block is in auxin synthesis, the auxin being required for the formation of DNA; 3) that the effect of the radiation is on an undefined entity in a reaction previous to and essential for both DNA and auxin synthesis. We are disregarding the possibility that the inhibition of both auxin and DNA synthesis is caused by dissimilar and unrelated radiation blocks. This omission is based on the similar dose responses and recoveries of the two systems.

The probability is low that the first of these interpretations is correct. This generalization is based on the following considerations. (1) Went's famous dictum "Ohne Wuchstoff kein Wachstum" has yet to be disproved. Without auxin, either endogenously synthesized or exogenously supplied, plant tissues will neither grow nor anabolize DNA (Skoog, 1954). (2) It is difficult to visualize how a reduction of DNA concentration in the nucleus can be manifest within minutes as a major loss in activity of a cytoplasmic enzyme. DNA synthesis is restricted to the nucleus, the synthesis of auxin to the cytoplasm. (3) The tips of coleoptiles are embryonic in ontogeny, although they are completely non-meristematic for ca. 2 to 3 days. Auxin synthesis in these organs is restricted to the tip. Yet the tips remain sites of auxin synthesis in this period although further elaboration of DNA has ceased.

These considerations as a whole suggest the second of the possibilities in Figure 9. The findings of Holmes et al. (1955) in Fig. 10, showing the DNA content of *Vicia* root tips as a function of distance from the tip, are pertinent in this connection. It is evident that the DNA content per cell increases with distance from the root apex, being about 30 percent greater in the fully elongated cell than in the cells of the terminal meristematic segment. In other words, DNA synthesis goes on in cells that do not synthesize auxin. At first glance this might seem to contradict the requirement of auxin synthesis for DNA elaboration. That it does not may be deduced from the fact that auxin is transported basipolarly from the production site at the tip to and through the cells comprising the region of elongation. Hormonal transport should satisfy any requirement for DNA synthesis.

Possibility number three would suggest an almost simultaneous effect in both the nucleus and

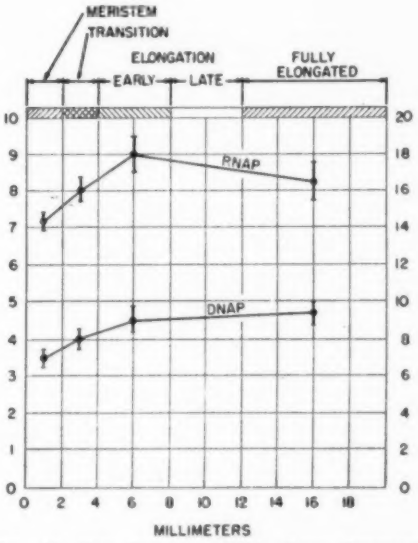

FIG. 10. THE RELATIVE DNA (LEFT ORDINATE) AND RNA (RIGHT ORDINATE) CONTENT PER CELL AT DIFFERENT DISTANCES FROM THE TIP OF *VICIA FABA* ROOTS.
(After Holmes, Mee, Hornsey, and Gray, 1955).

cytoplasm of a common molecular lesion. It is difficult to evaluate this simultaneity rigorously without exact studies of the time required between irradiation and inhibition of the two systems. In this connection, the work of Quastler, of Gray and Scholes, and our own, by completely separate approaches, all indicate that elongating cells are highly resistant to radiation damage. Since such cells do not synthesize auxin but evidently do synthesize DNA, it would be a fascinating problem to investigate whether the ability of elongating and differentiating tissues to synthesize DNA was impaired by ionizing radiation. It would certainly clarify the relationships outlined in Fig. 9.

In conclusion, I hope I have brought into focus one of the fundamental enigmas in the field of radiation effects: how so little energy, absorbed with virtually no specificity, can trigger the sequence of phenomena that constitute the radiation syndrome. The worker with plants is fortunate in having on hand two radiosensitive biochemical reactions—reactions that are both chemically characterizable and immediately sensitive to low radiation doses. He is also fortunate that these reactions play so essential a metabolic role that they facilitate our interpretation of the morphologic response of the plant, and possibly also the animal, to ionizing radiation.

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II. THE EFFECT OF IONIZING RADIATION ON CHROMOSOMES

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IT HAS long been known that ionizing radiation will cause chromosome aberrations, but only in recent decades have the cytological techniques been developed which will permit quantitative studies. Our work with *Tradescantia* microspore chromosomes was started twenty years ago, following the introduction of this genus into the Bussey greenhouse for cytotaxonomic work by Edgar Anderson. Much of the work reported here has been done by former graduate students, post-doctoral fellows and research assistants—Herbert Riley, Charles Rick, Norman Giles, Carl Swanson, Arnold Sparrow, Alan Conger, Charles Bishop, Sheldon Wolff, Edward King and Henry Luippold.

Ionizing radiation produces three general classes of aberrations depending upon the stage of nuclear development at the time of irradiation. Irradiation at the resting stage results in chromosome aberrations. At this stage of the nuclear cycle the chromosomes respond to irradiation as if they were single strands, and at metaphase and anaphase the induced aberrations are seen to involve both of the two sister chromatids. The chromosome aberrations include dot deletions, rod deletions, dicentric chromosomes, and ring chromosomes. Inversions and free translocations are also produced, but usually it is difficult to detect them and they are not included among the aberrations recorded for statistical studies.

Irradiation at prophase results in chromatid aberrations. At this stage the chromosomes have divided into sister chromatids, and the irradiation may break both or only one of the two sister chromatids at any given locus. The chromatid aberrations include deletions of only one of the two chromatids, the deletion of both chromatids to form isochromatid aberrations, breaks and reunions in the chromatids of different chromosomes followed by illegitimate reunions to form chromatid dicentrics or chromatid exchanges, and breaks and reunions of chromatids of the same chromosome to form chromatid rings or exchanges. The chromatid exchanges, or translocations, can usually be detected only at metaphase, but the chromatid deletions, isochromatids, dicentrics and rings can be recognized at either metaphase or anaphase. Other types of chromatid aberrations are induced, but they are not readily detected or are so rare that they are not included in the records of aberration frequency.

Irradiation in very late prophase or prometaphase produces half-chromatid, or "subchromatid," aberrations. With the x-ray doses normally used (50–400 r) for inducing chromosome aberrations in *Tradescantia* microspores, half-chromatid aberrations are obscured by the stickiness of the chromosomes following irradiation. If, however, the dosage is reduced to 10–30 r, the stickiness persists for only a few hours after irradiation and chromatid aberrations can be detected at from 3 to 7 hours after raying. These include half-chromatid exchanges between sister chromatids and, more rarely, half-chromatid exchanges between chromatids of different chromosomes (Sax and King, 1955). They can be detected only at anaphase as a rule, and even at that stage the existence of half-chromatids is inferred from the nature of the aberration. In the meiotic chromosomes of *Lilium* (Crouse, 1954; Mitra, unpublished) and *Trillium* (Sparrow, unpublished), the nature of the x-ray induced half-chromatid aberrations is more evident.

The induced half-chromatid aberrations were first observed by Swanson (1947) in the pollen tube chromosomes of *Tradescantia*. They have recently been found in root tip cells following chemical treatment and may occur spontaneously. These observations were reviewed by La Cour and Rutishauser (1954), who found x-ray induced half-chromatid aberrations, or "point errors," in *Scilla* endosperm cells, and by Walters (1955), who observed spontaneous half-chromatid breaks at meiosis in interspecific hybrids of *Bromus*. The

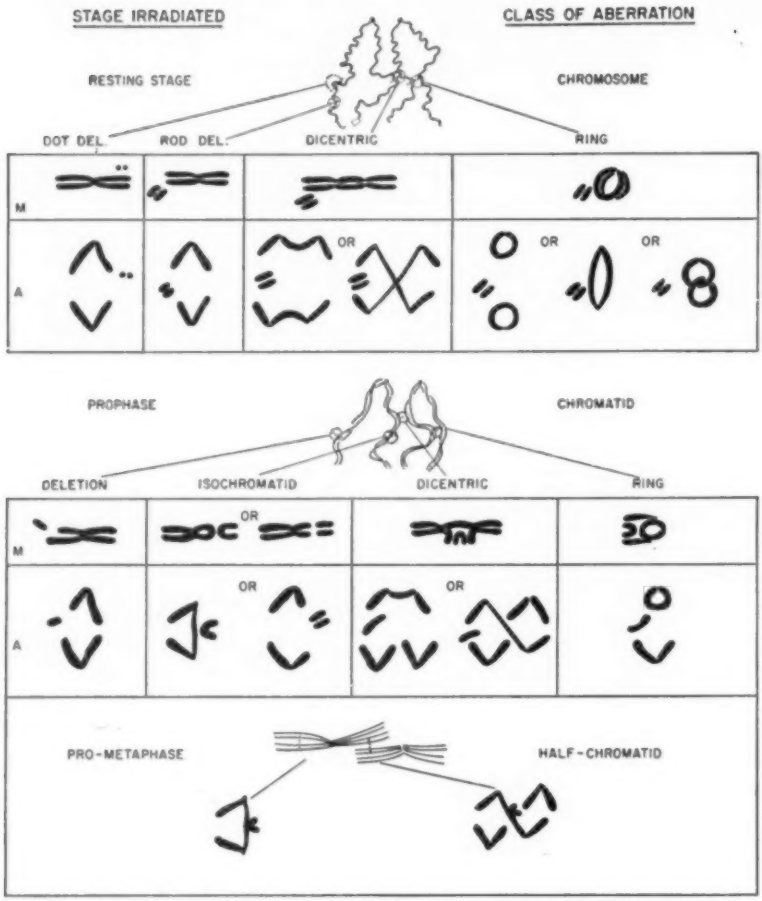

FIG. 1. MAJOR TYPES AND CLASSES OF CHROMOSOMAL ABERRATIONS INDUCED BY X-RAYS AT VARIOUS STAGES OF NUCLEAR DEVELOPMENT

origin and appearance of typical chromosome, chromatid and half-chromatid aberrations are shown in Fig. 1.

EFFECTS OF IONIZING RADIATION ON THE CELL CYCLE

It has long been known that cell division is inhibited by ionizing radiation. This effect is of importance in studies of radiation sensitivity at various stages of the cell cycle. Carlson (1950) has found that grasshopper neuroblasts are very sensitive to x-rays, and a depression of mitosis can be induced by as little as 4 r. The retardation of mitosis increases with increased dose. The suppression of mitosis and its recovery following an x-ray dose of 15 r is shown in Fig. 2.

The mitotic cycle in *Tradescantia* microspores is also suppressed by x-rays (Koller, 1943), but is less sensitive than that of grasshopper neuroblasts. With the relatively low doses used for irradiating prophase nuclei and with a period of four or five days between irradiation of resting nuclei and analysis of metaphase figures, the suppression of nuclear development by x-rays is of little significance in the types of aberrations produced at various stages in the nuclear cycle of *Tradescantia* microspores.

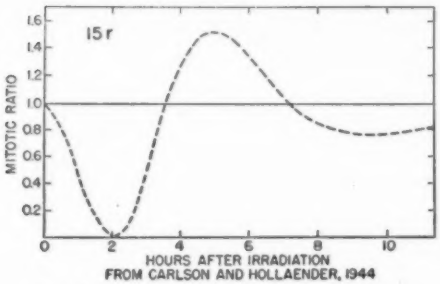

FIG. 2. EFFECT OF X-RAYS ON THE MITOTIC CYCLE IN GRASSHOPPER NEUROBLAST CELLS

CHROMOSOME DUPLICATION

The types of x-ray induced chromosomal aberrations induced at various stages of the nuclear cycle in *Tradescantia* microspores provide some evidence regarding the time and nature of chromosome duplication. In late spring, summer and early fall, the mitotic cycle covers about six days. Irradiation during the first four or five days produces only chromosome aberrations. Between 30 and 40 hours prior to metaphase, there is a transition from chromosome to chromatid aberration, as first observed by Riley (1936). Irradiation at 8 to 30 hours before metaphase produces chromatid aberrations, and at 4 to 6 hours only half-chromatid aberrations are produced. In any one inflorescence there is considerable variation in the stage of nuclear development since the divisions of the microspore nuclei are not synchronized, but it appears that sub-chromatid threads are differentiated with respect to breakage by ionizing radiation in very late prophase, as chromatids in early prophase, and as single strands during the resting stage.

The fact that only half-chromatid exchanges are found following irradiation at late prophase suggests that only one of the half-chromatids in each chromatid is subject to breakage or illegitimate reunion. Perhaps the broken ends of the newly formed half-chromatids restitute so quickly that they do not take part in illegitimate reunions. Recent work by Sax and King shows that half-chromatid aberrations are also induced by beta radiation with an ionization density considerably greater than that of x-rays.

The x-ray induced aberrations also provide evidence regarding relational coiling of the sister chromatids during the mitotic cycle. The sister chromatids appear to be twisted about each other at late prophase. If the DNA molecules are coiled in an interlocked spiral at the time of duplication a fantastic amount of uncoiling would be necessary to free the resulting sister chromatids, which usually lie more or less parallel to each other at metaphase. Yet, in half a dozen species, ring chromosomes have been found which divide regularly during the entire life cycle. If the ring chromosome is formed while the chromatids or sub-chromatids are relationally coiled, the daughter ring chromosomes would be so interlocked that they could not divide regularly. Yet the ring chromosomes, if small, usually separate freely at anaphase or, if large, may form a single ring or two interlocked rings at anaphase. The single or interlocked rings may break at anaphase and the broken ends reunite to form new rings (McClintock, 1941).

The relational coiling in ring chromosomes has been studied in *Tradescantia* microspores by inducing ring chromosomes at various times during the nuclear cycle. This work was done in late winter and early spring when the nuclear cycle covered a period of 8 or 9 days. Microspores irradiated 10 or 11 days before fixation were at meiosis, as indicated by the relatively high sterility of the microspores. Those rayed at 6 to 8 days before anaphase were in the early resting stage. Since the data on the frequency of types of rings were similar in these two series they have been combined. Microspores irradiated later in the resting stage showed essentially the same frequency of free rings, open rings and interlocked rings at anaphase (cf. Fig. 1) as those irradiated at late meiosis or early in the microspore resting stage (Table 1). The smaller ring chromosomes usually separated freely, but the larger ones were usually opened into a single ring at anaphase. There was little evidence of much relational coiling whether the rings were induced very early

TABLE 1

Types and frequencies of ring chromosomes induced by x-rays at late meiosis to the late resting stage of the microspore nucleus (Sax and King, 1956)

Time of Raying-Days Before Anaphase	Types of Rings		
	Free (%)	Open (%)	Interlocked (%)
11–6 days	125 (52)	63 (26)	52 (22)
4–3 days	69 (53)	38 (29)	23 (18)

in the nuclear cycle or towards the end of the resting stage.

DIFFERENTIAL SENSITIVITY

Chromosomes show great variation in their sensitivity to ionizing radiation at different periods in the nuclear cycle of mitosis and meiosis. The resting stage is most resistant to x-rays as measured by the frequency of chromosome aberrations. Sensitivity increases as the nucleus enters prophase and increases several fold at early prophase. Aberration frequency remains high during prophase of the *Tradescantia* microspore nuclei (Sax, 1941). The irradiation of metaphase chromosomes results in no immediately visible aberrations, presumably because the chromosomes at this stage are separated too far to permit union of broken ends in different chromosomes, and single breaks release no chromosome fragments until late telophase or early in the resting stage.

In order to analyze aberrations induced at metaphase and anaphase of the microspore nuclear division it is necessary to examine metaphase and anaphase divisions of the generative nucleus in the pollen tube. This was done by Bishop (1950), who found that metaphase and anaphase stages in the microspore division were about 10 times as sensitive to irradiation as was the post-mitotic resting stage and about 4 times as sensitive as the post-mitotic prophase preceding the division of the generative nucleus in the *Tradescantia* pollen tubes.

The earlier work of Sparrow (1944) had shown an even greater range of radiation sensitivity in the meiotic chromosomes of *Trillium*, and the results of more recent work by Sparrow, Moses and Dubow (1952) are shown in Fig. 3. Sensitivity, as measured by fragments induced by 50 r of x-rays, was greatest at meiotic prophase, declining during first and second meiotic divisions and reaching the lowest degree of sensitivity at the resting stage of the microspore nucleus about 7 days after meiosis. The diplotene chromosomes were about 60 times as sensitive as those in the microspore resting stage. This and other evidence shows that meiotic chromosomes are more sensitive than mitotic chromosomes and that chromosomes at the time of nuclear division are much more sensitive than they are during the resting stage.

It has been suggested that differential sensitivity at various stages of the nuclear cycle is associated with chemical changes in the chromosomes, and particularly with the concentration of DNA, but there is little evidence to support this assumption. There is an increase in sensitivity at early prophase following the differentiation of the chromosomes into sister chromatids and at about the time of DNA synthesis in *Tradescantia* microspores (Tay-

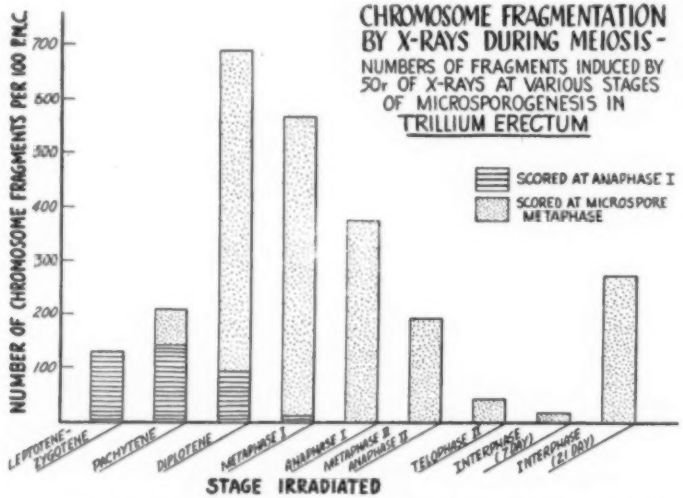

FIG. 3. FREQUENCY OF CHROMOSOMAL ABERRATIONS INDUCED BY X-RAYS AT VARIOUS STAGES OF NUCLEAR DEVELOPMENT AT MEIOSIS AND MITOSIS IN TRILLIUM
(From Sparrow, Moses and DuBow, 1952)

lor, 1953), but the peak of greatest sensitivity is at metaphase and anaphase, according to Bishop. Chemical changes can augment radiation sensitivity, as we shall show later, but there is little evidence that chemical changes within the chromosome are directly responsible for the differential sensitivity found during the nuclear cycle.

There is, however, evidence that physical factors play an important part in differential sensitivity to radiation at different periods in the nuclear cycle. In somatic cells, the period of minimum sensitivity at prophase is associated with the differentiation of chromatids, initiation of the coiling system and of chromosome contraction, and chromosome movement. The peak of sensitivity at late prophase, metaphase and anaphase is at a stage where the chromosomes are under the stress of minor coiling and both lateral and longitudinal stress in metaphase orientation and anaphase separation.

In the meiotic cycle of *Trillium* the peak of sensitivity is at diplotene where the chromosomes are under the stress of the coiling mechanism, repulsion of the paired homologues, and orientation of pairs of chromosomes. The experimental evidence from centrifugation and sonic radiation during irradiation supports the interpretation that differential sensitivity is due in part to physical movement.

THE EFFECT OF CENTRIFUGATION

The effect of stress upon the chromosomes during irradiation was tested by x-raying *Tradescantia* inflorescences while they were being centrifuged at 2080 r.p.m. The control inflorescences were irradiated in the centrifuge tubes either held stationary in a horizontal position or rotated slowly at 400 r.p.m. In other experiments the inflorescences were subject to centrifugation only after irradiation. Centrifugation during irradiation greatly increased the frequency of both chromosome and chromatid aberrations. When centrifuged after irradiation, beginning about 5 minutes after raying, there was little or no effect (Sax, 1943). If, however, irradiation is followed immediately by centrifugation of the *Tradescantia* microspores there is an increase of aberration frequency, but not as great an increase as when centrifuged during irradiation (Wolff and von Borstel, 1954). These results indicate that the broken ends of the chromosomes are separated by centrifugation, inhibiting restitution and promoting illegitimate fusion, and that the effects of post-centrifugation immediately after raying are effective because some of the induced breaks remain open for several minutes after irradiation.

Wolff and von Borstel found in both *Tradescantia* and *Vicia* that centrifugation for 15 minutes before irradiation decreased the aberration frequency several-fold. This effect is attributed to the compression of the chromosomes and the hindrance of motion which promotes restitution of broken ends of the chromosomes.

THE EFFECTS OF SONIC RADIATION

Further evidence on the effect of induced chromosome movement in increasing chromosome aberrations produced by x-rays has been provided by Conger (1948). No aberrations were produced in *Tradescantia* microspores subjected to sonic energy from an electronic oscillator operating at about 9000 cycles per second, but simultaneous exposure to x-rays and sonic energy increased chromosome aberrations about 30 percent above the frequency from exposure to x-rays alone. The increased frequency of aberrations is attributed by Conger to the movement of the chromosomes induced by the sonic energy and thus decreasing the chances of restitution and increasing the chances of illegitimate reunions between the broken ends of the chromosomes.

DOSAGE RELATIONSHIPS

The relation between dosage and the frequency of the various types of x-ray induced chromatid and chromosome aberrations has provided critical information regarding the mechanism of aberration formation. The fact that the simple deletions show a linear relationship to x-ray dosage indicates that these aberrations are the result of a single reaction or "hit." The more complex ring dicentric and exchange aberrations tend to increase as the square of the dosage, indicating that they are largely the result of two independent events or "hits" (Sax, 1941). The chromosome dot deletions (Rick, 1940), and the isochromatid deletions (Catcheside, Lea and Thoday, 1946), are predominantly the result of single "hits," but the fact that the exponent of the dosage curve equation is significantly greater than 1.0 indicates that some are produced by two independent "hits." The relationships between x-ray dosage and the "one-hit" and "two-hit" aberrations are shown in Fig. 4.

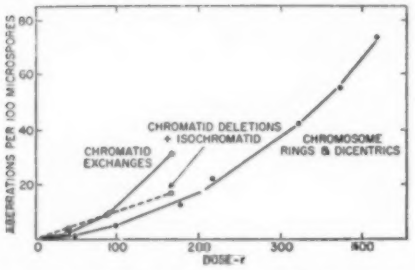

FIG. 4. RELATION BETWEEN X-RAY DOSE AND FREQUENCY OF THE DIFFERENT TYPES AND CLASSES OF CHROMOSOMAL ABERRATIONS INDUCED IN TRADESCANTIA MICROSPORES

THE EFFECT OF DOSAGE INTENSITY

The frequency of "one-hit" aberrations induced by a given dose of x-rays is essentially the same regardless of radiation intensity, but the frequency of "two-hit" aberrations is dependent upon the intensity of the radiation. Irradiation at high intensities produces more ring and dicentric aberrations than does the same dose at low intensities. A dose of 480 r at 160 r/minute produced twice as many ring and dicentric chromosomes as the same dose at 2.7 r/minute, as is shown in Fig. 5 (Sax, 1941). This intensity effect is attributed to the time factor in the production of "two-hit" aberrations.

We would not expect that the number of breaks induced would be dependent upon radiation intensity. This assumption is confirmed by the lack of an intensity effect on the simple "one-hit" deletions. But the "two-hit" aberrations are dependent upon two independent breaks followed by illegitimate union of broken ends of chromosomes or chromatids. If the radiation is given rapidly the first break remains open until a second break occurs in an adjacent chromatid or chromosome, thus permitting illegitimate unions. If, however, the radiation is given slowly, the first break may undergo restitution before the second break occurs, thus allowing no opportunity for illegitimate union; the second break will either undergo restitution or result in a simple terminal, or "one-hit," deletion.

The relation between dosage and the frequency of "two-hit" aberrations is also dependent upon dosage intensity. At high intensities the aberration frequency tends to increase as the square of the dosage, but the exponent is usually no more than 1.8–1.9. At very low intensities the exponent may drop to 1.5 or less. Catcheside, Lea and Thoday (1946) have determined the "one-hit" components of the frequencies of chromatid exchanges induced by 150 r of x-rays at high and low intensities. At 125 r/minute the "one-hit" component was negligible in the total exchanges produced, but at 0.6 r/minute the "one-hit" exchanges constituted about a third of the total aberrations. At the lower intensity the total aberration frequency was less than half of that at the higher intensity.

Irradiation of *Vicia* root tip chromosomes at very high intensities produced a marked increase in the frequency of "two-hit" aberrations (Wolff and Luippold, 1956). A dose of 600 r given in one-half minute produced an aberration frequency about 50 per cent greater than the same dose given in 3 minutes. This effect is attributed to breaks in ionic bonds which restitute so rapidly that they produce no aberrations at x-ray intensities commonly used.

THE EFFECT OF FRACTIONATED DOSAGE

If the decrease in the frequency of "two-hit" aberrations at low intensities of x-rays is due to the restitution of one break before an adjacent break is produced, the fractionation of the dose should also decrease the frequency of "two-hit" aberrations. The duration of the rest periods between exposures should also provide evidence regarding the duration of "open" breaks.

Tradescantia microspores were irradiated at 25 r/minute for 4 minutes to establish a base line for comparison of aberration frequencies induced by 16-minute exposures given in a single dose and in

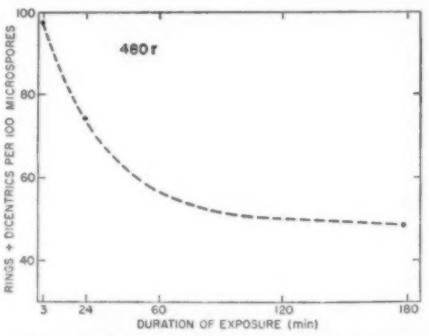

FIG. 5. THE RELATION BETWEEN DOSAGE INTENSITY AND THE FREQUENCY OF 2-HIT CHROMOSOME ABERRATIONS IN TRADESCANTIA MICROSPORES

four fractionated doses with various rest periods. The base line was determined by multiplying the aberration frequency induced by a single exposure by 4. If the aberrations produced by the four fractionated exposures do not exceed those of the base line it indicates that no breaks induced by a fractionated exposure remain open to unite with breaks induced by a subsequent exposure. If the four fractionated exposures induce aberration frequencies above the base line, some of the breaks induced by a fractional exposure must have remained "open" to unite with breaks induced by a subsequent exposure. With increasing duration of rest periods between exposures the aberration frequencies should decline to the level of the base line, thus indicating the period during which the breaks can remain "open."

In the early experiments (Sax, 1939) it was found that a single complete exposure produced an aberration frequency much higher than that of the base line, and that the frequency induced by fractional dosage declined with successively longer rest periods. For chromosome aberrations (rings and dicentrics) the frequency reached the base line with the rest periods of about an hour, although there was considerable variation at different x-ray intensities. The two-hit chromatid aberration frequency reached the base line with rest periods of about 10 minutes, and the average duration of "open" chromatid breaks was found to be about 5 minutes.

The decrease in aberration frequency resulting from fractionated x-ray dosage has also been attributed to cell injury. According to Lane (1953), the injury induced by the first exposure makes the chromosomes less sensitive to the second exposure. With sufficiently long rest periods, the nucleus recovers its sensitivity to the second exposure. A similar interpretation has been used by Koller (1953) to explain the decrease in the frequency of chromosome aberrations when the cells are irradiated at low x-ray intensities. There is some evidence to indicate that cell injury may be involved as a minor factor in fractionated dosage effects in *Tradescantia* (Fig. 6 after Sax, King and Luippold, 1955) and in barley (Caldecott and Smith, 1952). However, the experiments of Sax and Luippold (1952), De Serres and Giles (1953), Steffensen and Arnason (1953), and Bora (1955) indicate that the effect of fractionated dosage is due largely or entirely to the restitution of chromosome breaks during the rest periods.

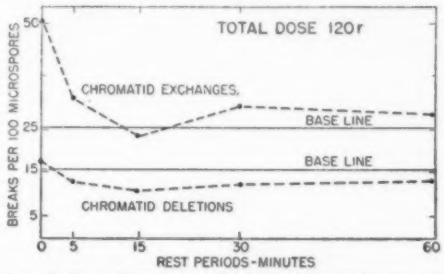

FIG. 6. THE EFFECT OF FRACTIONATED DOSAGE ON THE FREQUENCY OF 1-HIT AND 2-HIT CHROMATID ABERRATIONS INDUCED IN TRADESCANTIA.

The fractionated doses were given in 4 exposures with rest periods between exposures of 5, 15, 30 and 60 minutes. The base lines were determined by obtaining the aberration frequency from a single exposure and multiplying this value by 4.

THE EFFECT OF IONIZATION DENSITY

The early work of Giles (1940) showed that more chromosome aberrations were produced by neutrons than by comparable doses of x-rays as measured by equal amounts of ionization. It was also found that low energy neutrons of 7.5 Mev were more efficient in producing chromosome aberrations than high energy neutrons of 15 Mev (Giles, 1943). Fast neutrons from the Oak Ridge pile with an average energy of 1.0 Mev were found to be about twice as effective as the 7.5 Mev neutrons from the Yale cyclotron (Giles and Conger, 1950). Kotval and Gray (1947) found that alpha radiation was more effective than neutrons in producing chromosome aberrations. Kirby-Smith and Daniels (1953) found that medium energy x-rays of 60 kev were more effective than Co^{60} gamma rays or 400 kev mean energy beta rays in producing chromosome aberrations. The effectiveness of ionizing radiation is directly related to the average rate of energy loss per micron of track in the plant nucleus, as is shown in Fig. 7, from Conger, Randolph and Johnston (unpublished).

Irradiation with alpha rays or neutrons shows a linear relationship between dosage and the frequency of "two-hit" aberrations, although such aberrations induced by x-rays, given at high intensities, tend to increase in proportion to the square of the dose. The difference is attributed to the higher ionization density of the recoil proton or of the alpha track which results in simultaneous breaks of both adjacent chromosomes of chromatids within the critical area of illegitimate reunion.

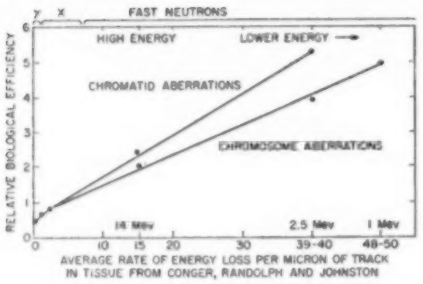
γ X FAST NEUTRONS
HIGH ENERGY
LOWER ENERGY
CHROMATID ABERRATIONS
CHROMOSOME ABERRATIONS
RELATIVE BIOLOGICAL EFFICIENCY
14 Mev
2.5 Mev
1 Mev
0 10 15 20 30 39-40 48-50
AVERAGE RATE OF ENERGY LOSS PER MICRON OF TRACK IN TISSUE FROM CONGER, RANDOLPH AND JOHNSTON

FIG. 7. THE EFFECT OF IONIZING RADIATION OF DIFFERENT ENERGIES ON THEIR RELATIVE EFFICIENCY IN INDUCING CHROMOSOMAL ABERRATIONS IN TRADESCANTIA MICROSPORES

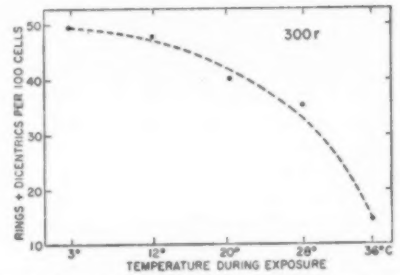

FIG. 8. THE EFFECT OF TEMPERATURE AT THE TIME OF X-RAYING ON THE FREQUENCY OF CHROMOSOME ABERRATIONS INDUCED IN TRADESCANTIA MICROSPORES

Kotval and Gray (1947) suggest that alpha particles which pass close to the chromosome thread as well as those which pass through it may cause chromosome breaks.

An analysis of the differences in effectiveness of x-rays and neutrons in inducing chromosome breakage had enabled Lea (1947) to conclude that the effective target area of ionizing radiation is about a micron in diameter, and that the number of ionizations required to produce a break are about 15–20.

THE TEMPERATURE EFFECT

Irradiation of *Tradescantia* microspores at low temperatures results in a higher frequency of chromosome aberrations than irradiation at high temperatures (Sax and Enzmann, 1939; Catcheside, Lea and Thoday, 1946). The effect of various temperatures on the frequency of ring and dicentric chromosomes induced by 300 r of x-rays is shown in Fig. 8. Irradiation at 3°C. resulted in more than three times as many aberrations as irradiation at 36°C. Temperature changes following irradiation were effective in some cases, but little effect was found in other experiments (Sax, 1947).

There was also considerable variation in the effect of temperature on the induction of chromatid aberrations. Microspores fixed at 48 hours after irradiation during the winter months produce both chromosome and chromatid aberrations. The chromosome aberration frequency was increased by irradiation at low temperature, but the chromatid aberration frequency was increased by irradiation at high temperatures. Microspores fixed at about 24 hours after irradiation showed a temperature effect in some experiments (Catcheside, Lea and Thoday, 1946), but not in others. Recent experiments by King (unpublished), replicated three times and involving an analysis of 15,000 chromosomes, showed little or no difference in the frequency of chromatid aberrations resulting from an x-ray dose of 50 r at 3° and at 32° C.

The temperature effect on chromosome aberrations is attributed to more rapid restitution of breaks induced at high temperatures, thus decreasing the opportunity for illegitimate union and the production of ring and dicentric chromosomes. The inconsistent response of chromatid aberrations to temperature may be due to the more rapid restitution of chromatid breaks, as is indicated by the duration of "open" breaks in chromosomes and chromatids in the fractionated dosage experiments.

At very low temperatures, −190°C., the chromosome aberration frequency is reduced in *Tradescantia* (Fabergé, 1954), and in barley (Nybom et al., 1953; Nilan, 1954).

THE EFFECT OF ANOXIA

Thoday and Read (1947) found that irradiation of *Vicia faba* root tips under anaerobic conditions greatly reduced the x-ray effects as measured both by growth inhibition and by the frequency of chromosome aberrations in the dividing cells. In *Tradescantia* microspores irradiated in a nitrogen atmosphere the aberration frequency was much lower than that resulting from irradiation in air (Giles and Riley, 1949). Irradiation in argon and helium also greatly reduced aberration frequency, showing that the effect was due to lack of oxygen and not of a particular gas, such as nitrogen (Riley and Giles, 1950).

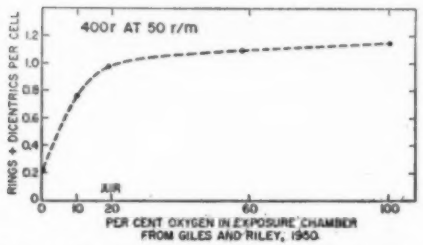

FIG. 9. THE EFFECT OF OXYGEN CONCENTRATION IN THE ATMOSPHERE AT THE TIME OF X-RAYING ON THE FREQUENCY OF CHROMOSOME ABERRATIONS INDUCED IN TRADESCANTIA MICROSPORES

The aberration frequency increases rapidly with an increase in oxygen up to about 20 per cent, and increases slowly as the percentage of oxygen is increased to 100, as is shown in Fig. 9. A slight further increase of aberrations was induced when the microspores were irradiated in 100 per cent oxygen at a pressure of 1500 mm. of mercury.

The oxygen effect has been attributed to an increase in the number of breaks during irradiation since the immediate introduction of oxygen into the exposure chamber after irradiating in vacuum has no effect in increasing aberration frequency. Riley, Giles and Beatty (1952) found no effect of oxygen concentration on the time of restitution of breaks in *Tradescantia* microspore chromosomes, but Wolff (1954), working with *Vicia* root tip chromosomes, found more rapid restitution of x-ray induced breaks under anoxia. Swanson (1955) found the oxygen effect to be related to the energy of the ionizing radiation and suggested that the major effect of oxygen is related to the fate of latent breaks induced by the ionizing radiation.

High concentrations of oxygen over longer periods of time appear to cause chromosome aberrations. This strictly oxygen effect cannot be observed with *Tradescantia* inflorescences because of the lethal effect, but in dried pollen grains exposure to 100 per cent oxygen for an hour produced as many chromosomal aberrations as approximately 1200 r of x-rays (Conger and Fairchild, 1952).

THE EFFECT OF CO AND CO_2

The exposure of *Tradescantia* microspores to positive pressures of CO or CO_2 alone does not result in chromosomal aberrations, and when the inflorescences are irradiated while in an atmosphere of CO or CO_2 the aberration frequency is no greater than when irradiated in an atmosphere of an indifferent gas such as nitrogen. If, however, the microspores are irradiated in an atmosphere of air plus positive pressures of CO or CO_2 the chromosome aberration frequency is much greater than that resulting from irradiation in air (King, Schneiderman and Sax, 1951; Schneiderman and King, 1953).

The increase in aberration frequency when the microspores are exposed to CO depends on the time of exposure to the gas prior to irradiation, reaching a maximum after about one hour of exposure. But the CO must also be present during irradiation to be effective in increasing aberration frequency. The CO effect is largely inhibited by the pressure of high concentrations of oxygen, yet oxygen promotes chromosome breakage. The aberration frequency was not increased when the microspores were subjected to a CO atmosphere within 30 seconds after irradiation, indicating that the CO affects the breakage mechanism rather than the restitution process.

If the production of chromosomal aberrations is associated with H_2O_2 production the CO effect could be attributed to the inhibition of cytochrome oxidase causing the flavoproteins to produce more H_2O_2. High oxygen tensions increase the activity of the terminal oxidases, but oxygen inhibits the CO effect, presumably by reversing the CO inhibition of cytochrome oxidase.

Carbon dioxide also is effective in increasing the frequency of x-ray induced aberrations only during irradiation and in the presence of oxygen. In mixtures of air plus increasing pressures of CO_2 the aberration frequency increases with increased pressures of CO_2, as shown in Fig. 10. The available data permit no conclusions regarding the mecha-

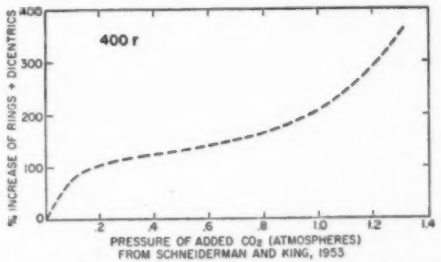

FIG. 10. THE EFFECT OF ADDED CO_2 TO THE ATMOSPHERE DURING X-RAYING ON THE FREQUENCY OF CHROMOSOME ABERRATIONS INDUCED IN TRADESCANTIA MICROSPORES

nism of the CO_2 effect, and the suggested mechanism of the CO effect has been questioned.

THE EFFECT OF INFRA-RED RADIATION

Irradiation with infra-red alone has no visible effect on the chromosomes, but does increase the frequency of chromosomal aberrations induced by x-rays if given either before or after exposures to x-rays. Swanson (1949) found that irradiation of *Tradescantia* microspores for 3 hours greatly increased the total chromatid aberrations induced by subsequent exposures to x-rays, even when the infra-red treatment was given as much as 96 hours prior to x-irradiation. Infra-red was also effective when given after exposures of x-rays, even with a delay of as much as 15 hours. The fact that the infra-red effect occurs long after the normal time limit of restitution, or recombination, of x-ray induced chromatid breaks indicates that the effect of infra-red may delay restitution, permitting more chromatid deletions and exchanges. But, the fact that infra-red exposures as much as 96 hours before x-irradiation are effective in increasing aberration frequency indicates that the infra-red effect is caused by activating the chromosome bonds so that they are more sensitive to x-ray breakage. Further evidence to support the activated state hypothesis has been presented by Yost (1952), but the mechanism of the infra-red effect is unknown.

THE EFFECT OF CHEMICALS

The treatment of irradiated cells with various chemicals may increase or decrease the frequency of chromosomal aberrations induced by x-rays. Root tip cells have been used in these experiments because the chemicals do not reach the microspores within the necessary time limit when the stems of *Tradescantia* inflorescences are placed in the solutions.

The frequency of chromosomal aberrations is reduced by cysteine (Forssberg and Nybom, 1953) and by sodium hydrosulfite (Riley, 1952), in *Allium*. Mikaelsen (1954) found that chromosomal aberrations induced by x-rays in *Tradescantia* root tip cells were reduced by cysteine and by sodium cyanide, while in *Vicia* Wolff (1954) found a protective effect of 2,3-dimercaptopropanol (BAL). These chemicals appear to act as oxygen acceptors and by reducing oxygen tension in the cells promote the restitution of x-ray induced breaks and decrease aberration frequency.

Mazia (1954) found that ethylenediamine tetraacetic acid (Versene) was effective in promoting chromosome breakage in *Drosophila* and *Melanoplus*. The effect was attributed to the chelating effect of the Versene in withholding the calcium and magnesium ions presumably involved in bonds uniting the chromosome units. Steffensen (1955) observed that the amount of chromosome breakage induced by calcium deficiency plus the breakage induced by x-rays was less than the combined effect of calcium deficiency and x-irradiation. Similar results have been found by Wolff and Luippold (1956). Versene alone will induce chromosomal aberrations in *Vicia*, but root tips subjected to Versene and x-rays simultaneously show more chromosome aberrations than the additive effect of Versene and x-rays. The role of ionic bonds in chromosome breakage is also supported by the very rapid restitution of certain types of breaks revealed only by x-ray dosage of very high intensity (Fig. 11).

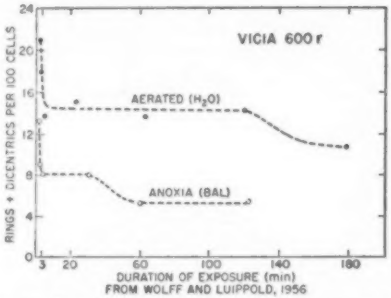

FIG. 11. THE EFFECT OF RADIATION INTENSITY AND OF INDUCED ANOXIA ON THE FREQUENCY OF CHROMOSOME ABERRATIONS INDUCED BY X-RAYS IN *VICIA FABA* ROOT TIP CELLS

CONCLUSIONS

Cytological studies of chromosome breakage induced by ionizing radiation at various stages of nuclear development have provided evidence regarding the time of chromosome duplication and the nature of chromosome breakage and reunion.

The types and frequencies of chromosome aberrations induced by radiation of different ionization densities and dosage intensity support the target theory of Lea.

The frequency of chromosomal aberrations induced by a given dose of x-rays is dependent upon the nuclear stage irradiated and can be modified by varying the temperature of the cells during irradiation, by varying the dosage intensity, by fractionated dosage, by centrifugation of the cells during irradiation, by irradiating the cells with

infra-red before or after x-irradiation, by anoxia, by irradiating the cells in atmospheres of CO or CO_2, and by treating the cells with various chemical agents. Neutrons and α-radiation are more effective than x-rays in producing chromosomal aberrations because of the higher density of the ionization track. They produce the same types of chromosomal aberrations as do x- or γ- radiation, but the dosage relationships are different.

The modifying mechanisms or agencies which increase or decrease the frequency of chromosomal aberrations generally, although not invariably, also modify radiation injury to cells and organisms. The nature and action of such protective agencies are of obvious importance in this atomic age. The agents which augment radiation sensitivity, such as CO_2, might well be applicable to radiation therapy. Radiation cytology can be of service in many areas of biological research.

ACKNOWLEDGMENT

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III. GENETIC EFFECTS OF RADIATION ON HIGHER PLANTS

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INTRODUCTION

IT WAS established almost 30 years ago, by Muller and Stadler, that hereditary changes similar to those occurring naturally could be induced in animals and plants by radiation. Since that time, radiation has been applied extensively in fundamental research on plants. Relatively little work was done in this country, however, to use radiation as a tool for plant breeding until almost the 1950's because it was believed by many geneticists that radiation caused only destructive genetic changes. The recent, more optimistic attitude toward the use of radiations for plant improvement has been due to at least four factors: (1) the persistent, successful efforts of European (mostly Swedish and German) workers in producing useful plant mutations, (2) the greater availability of radiation sources and an interest in finding peaceful uses for atomic energy, (3) our generally increased knowledge of hereditary materials, and (4) the production at a number of laboratories in this country of mutants having special significance to practical plant breeders.

Important in any appreciation of the biological effects and potential uses of radiation is an understanding of the manner by which radiant energy is transferred to cell components. Of principal interest is how changes are induced in the location, assemblage and composition of genetic units, and the relationship of these genetic units to the specific kinds of information they do or do not transfer. The true nature of induced genetic changes cannot now be defined, however, although recent data on the chemical and physical construction of the chromosome, together with the modern interpretation of chromosome organization, now provide the foundation for a view of genic variation that may prove to be enlightening.

Once it has been established that beneficial or useful mutants of agricultural plants can be produced, the main problem to be considered is whether they can be produced economically enough to warrant more general application of mutagenic agents in plant breeding. Destructive changes, including mutants of no practical value, make up the majority of readily detected alterations. These can be obtained in abundance for use in genetic studies by employing the simplest of present methods. In most cases, however, assurance that useful variants will be found can be had only if very large numbers of plants are tested.

The genetic effect of radiations can be modified by varying a number of environmental and physiological factors. By proper manipulation of such factors as temperature, gas phase, and moisture content—along with treatments with any one or more of a whole arsenal of radiations and mutagenic chemical compounds—far more efficient methods for the production of desirable mutations can certainly be developed. Research in this area is a prime need.

ENERGY DISSIPATION IN TISSUE BY RADIATIONS

The means by which different radiations cause changes in biological materials is still not clearly understood, but certain views of the way by which energy from radiation is dissipated within the cell seem agreed upon. Energy from radiation may be dissipated by a process of ionization in which electrons are ejected from atoms or molecules, and through excitations which raise the electrons of a molecule to higher energy levels. In each case chemical reactivity is increased.

Six different radiations generally available for radiobiological experiments are: ultraviolet, x- and gamma rays, beta particles or cathode rays, protons, alpha particles, and slow and fast neutrons. Ultraviolet light (wave length about 2537 Å from a mercury vapor germicidal lamp) is limited in its tissue-penetrating ability. In genetic experiments on plants its use is restricted to spores or pollen grains. The absorption of ultraviolet in the range

mentioned depends to a considerable extent on molecular structure, and is, for example, greater for nucleic acid than protein. The energy in each quantum of UV light is not sufficiently great to induce ionization, hence any biological effects produced are due almost exclusively to excitation.

X-rays and gamma rays are similar to ultraviolet light in that they, too, are electromagnetic short wave radiations. The former two, however, make up the lower end of the electromagnetic spectrum and are more alike in their action. In the main, gamma rays (from natural or artificial radioisotopes such as Co^{60}) have a shorter wave length and possess more energy than x-rays. Monoenergetic gamma radiation is usually obtained from radioisotopes, but frequently rays with two or more energies are emitted. This is in contrast to x-rays, which are generally produced in a broad range of energies. The soft x-rays of longer wave length (10 to 1 Å) are less penetrating, but more densely ionizing, than the shorter wave length (0.1 to 0.05 Å) hard x-rays. Through the use of high voltages and appropriate filters which absorb the soft radiation, high energy radiation similar to gamma rays can be obtained. In the energy range used for most biological experiments (below 2 Mev), x- and gamma rays transfer their energy to tissue through ionizations and through excitations of atoms or molecules.

Ionizations are produced principally by two mechanisms, photoelectric absorption and Compton effect interactions, with the relative contribution of each depending on the incident energy of the radiation. With the lower energy soft x-rays, photoelectric absorption is most important. In this process, atoms absorb energy quanta from the radiation, and electrons are ejected. Photons must have energy equal to or greater than the binding energy of an atomic electron in order to be absorbed by the atom and cause the release of the particle from its orbit. The Compton effect also results in the expulsion of electrons, but high energy photons of radiation are principally involved. In this type of interaction photons are scattered with reduced energy as the ejected electrons recoil with energy gained from the collision. With its remaining energy, the photon can carry out further Compton or photoelectric interactions until its energy is completely dissipated. The energized recoil electron, like the photoelectron, produces further ionizations by means of Coulomb force interactions as it passes through tissue. It is considered that the overwhelming percentage of biological effects is due to these secondary interactions with other electrons. The path of an electron in tissue is relatively short, but the distance between successive ionizations depends on the speed of the particle, i.e., as the particle loses more and more of its energy and slows down, the average density of ionizations along its path increases.

Except for their lower penetrating ability, beta particles (electrons) such as those from P^{32} and S^{35}, produce nearly the same effects in tissue as x- or gamma rays. However, the special characteristic of these sources is that they may be incorporated directly in the cell molecules, giving a somewhat greater localization of the site of action (Thompson et al., 1950; Kaplan and Michaelis, 1953).

The positively charged protons and alpha particles are much larger than electrons and produce a shorter, but more dense, path of ions through tissue. The energy of these particles is imparted to electrons via Coulomb forces of attraction rather than by repulsion, but the result is essentially the same so far as the kind of energy dissipation is concerned. Similarly, while excitation is also one of the effects produced by these radiations, the ionizations produced probably are the most important.

The non-charged particles, neutrons (obtained mostly from nuclear fission reactions in an atomic pile), do not cause ionizations directly. The more energetic fast neutrons release their energy in elastic collisions with nuclei of atoms present in the tissue. The collisions in tissue that are most effective from a biological standpoint are with hydrogen because it is the most abundant component element of tissue, and because maximum energy transfer occurs in collisions between particles equal in mass, a situation which is very nearly realized for the neutron and the proton of the hydrogen nucleus. As the energy of the neutron is reduced, however, the amount it can relay to protons of hydrogen nuclei becomes less and less at the same time that the probability for nuclear capture reactions increases. The slow, or thermal, neutron which eventually results, or which can be employed initially, may be captured by and cause transmutation of certain specific atomic nuclei with a consequent release of gamma rays, alpha or beta particles, or protons. The principal nuclear transmutations by thermal neutrons in tissue are those with nitrogen which ejects a proton, with an iso-

tope of boron which ejects an alpha particle, and with hydrogen which emits a gamma ray. These nuclear reactions are important biologically because the element involved is either abundant in the tissue, has a high cross-section or affinity for neutrons, or the half-life (time required to reduce activity by one-half) is short. The linear energy transferred per unit length of track in tissue (L.E.T.) is greater for alpha particles than protons and greater for protons than electrons (Zirkle, 1954). This is one of the most important physical factors influencing the biological effect of an ionizing radiation.

Stated more simply, all radiations cause genetic effects by transferring their energy to atoms or molecules present in or near the cell nucleus. This energy may cause ionization, involving the ejection of atomic electrons, or may produce molecular excitations by raising the energy state of cell constituents affected. The result is to enhance strongly chemical reactivity in that portion of the cell traversed by radiation or its products.

The site of energy dissipation is largely determined by chance and the properties of the radiation. Chemical changes may be produced in the cell via two general mechanisms. The first or direct action, in which the specific molecule undergoing change becomes ionized or excited when traversed by an electron, is distinguished from the second or indirect action, in which the molecule concerned does not absorb the energy itself but obtains it by transfer from another molecule. The relative importance of these mechanisms, which as yet has not been fully resolved, has evoked much controversy over the past several years. The basis for controversy may be illustrated by the fact that most of the genetic effect of radiation on dormant barley seeds appears to be the result of direct effects (Caldecott, 1955), whereas radiation damage to bacteria or *Neurospora* spores can be induced by mere irradiation of the medium or liquid in which the cells may be subsequently suspended (general references: Lea, 1946; Giles and Bolomey, 1948; Mayneord, 1950; Stapleton and Hollaender, 1952; Gray, 1954; Bacq and Alexander, 1955; Hurst et al., 1956; and Hine and Brownell, 1956).

MUTATIONS AND THEIR GENETIC NATURE

Our present knowledge of the self-duplicating chromosomal units, called genes, does not permit us to define the exact nature of the mutation process. However, we may derive some useful concepts of the mechanisms responsible for these hereditary changes by inference from available data. But first, what is a mutation? Exact interpretations of the word seem to depend on how conservative or how liberal the investigator prefers to be and on the biological object with which he works. Various authors use modifying adjectives such as "point" or "true" to describe and categorize mutational events not accompanied by cytologically visible changes and call all events associated with such changes pseudo-mutations or aberrations. Others make little effort to classify genetic changes, presumably because of inadequate cytological analysis. The ultimate understanding of relationships between cytological phenomena and the nature of mutations, nevertheless, has special significance in relation to the development of a fundamental concept of chromosomal organization.

Chromosomal alterations are readily induced with radiations and have been considered by some as separate phenomena from gene mutations. However, it seems more reasonable to believe that the several classifications of cytogenetic changes are not mutually exclusive but instead may well reflect only differences in the manifestation of a common basic event. MacKey (1956) also has expressed a similar view. One classification, for example, similar to that of Stubbe (1937), includes the following four categories of hereditary variations based on cytogenetic evidence: (1) gene mutations—viz., genetic changes characterized by the absence of cytologically visible alterations in the chromosomes (sometimes these have been called point mutations); (2) chromosome alterations—viz., detectable changes in chromosome structure, such as deletions, duplications, inversions, and translocations of genetic loci (a phenotypic effect may or may not be associated); (3) changes in chromosome number—this class includes types with increases or decreases in the number of whole chromosomes or sets of chromosomes, e.g. aneuploids and polyploids; and (4) cytoplasmic mutations, e.g., maternally inherited changes. All of these types have been described in radiation studies.

As we examine the data available to us at this time, the concept emerging is that a "gene" mutation is due not to a single phenomenon, but perhaps may be due to any one or more of a vast array of rather diverse phenomena. The intrinsic complexity of the genetic apparatus is such that we

should not attempt to oversimplify the whole of it when studying certain of its simple interactions.

The chromosome, according to the most acceptable model proposed recently in the field (Crick and Watson, 1954; Levine, 1955; Steffensen, 1957) is a structure made up of various species of DNA and protein molecules compounded together in helical form, with bonds between strands and cation bonds as links between protein and DNA or between DNA molecules (Brown and Watson, 1953). The stability of the divalent links in particular is thought to differ with the physiologic state of the cell or the stage of cell division. If this is so, the model helps to interpret such evidence as the ready breakability of the chromosome thread in certain types of cells. Steffensen, for example, has shown that the chromosomes of plants growing in a medium low in available calcium are more sensitive to both spontaneous and radiation-induced breakage. Furthermore, the fact that the chromosome seems to have a complex structure, as revealed by electron micrography (Ris, 1955; Kaufmann, 1948), helps to explain the delayed appearance of some induced chromosome breaks and mutations. Taylor, Woods and Hughes (1956) recently have obtained conclusive evidence that the half chromatids of a chromosome synthesize whole copies of themselves in the replication process during the mitotic cycle. Replicated chromosome parts do not contain a mixture of "new" and "old" chromosome material. In fact, the old chromosome apparently acts as a template on which "new" material is aligned and finally molded. This new evidence alone has considerable significance, but still there are few critical data on the intimate structure and components of the chromosome, and much less on the genetic units they carry.

For some more intensively studied genetic loci, at least, there appears to be a remarkable proximity of genetic material controlling particular kinds of reactions in the organism. In maize, for example, the yg_2 (yellow-green) locus is found in the chromomere nearest the knob on chromosome 9, and very near-by is another locus which also affects chlorophyll production (Dollinger, 1954; Schwartz, 1955). Moreover, components of the *R* locus and of the *A* locus in maize show pseudoallelic association (Laughnan, 1955; Stadler and Emmerling, 1956). Similar genetic associations also occur in *Drosophila*, bacteria, bacteriophage and *Neurospora* (Lewis, 1951; Demerec and Demerec, 1955; Benzer, 1955; Barratt et al., 1954).

In our view of the gene we cannot lose sight of the fact that while we recognize a gene by its absence or failure to function in a usual manner, other genetic loci in the same or in different chromosomes also must function to make either the normal or mutant effect possible. Often the whole of the organism is concerned, since the interaction of genes may differ with stage of development. Such a concept of the gene, given in terms of function, requires modification of earlier concepts of genes as discrete particles carried in the chromosome thread. Thus a gene, in terms of the biochemical approach to genetics, may be defined as that particular segment of a chromosome which permits or controls, by its presence, absence, or inactivation, the initiation or degree of completion of a particular (simple or complex) biochemical process.

What relationship has chromosome breakage not associated with any visible aberration to mutation? Available evidence seems to support the contention that mutation may or may not result following breakage of the chromosome, but also that breakage is not a prerequisite for mutation (MacKey, 1956; Muller, 1954a,b). A purine analogue, 9-D-riboside, is highly mutagenic, but does not increase sterility of barley plants (Ehrenberg et al., 1956), nor appear to cause structural aberrations (Kihlman, cf. MacKey, 1956). On the other hand, a detergent, Ceepryn, will induce chromosome breaks, but apparently not mutations (Smith and Lofty, 1954).

It is now known that a large proportion of mutations induced in higher plants by radiations are due to cytogenetic deficiencies. The evidence obtained earlier by McClintock (1931) and by Stadler (1940) and others is definite on this point. Looking at the data objectively, however, they actually represent recessive mutation types induced under a particular set of conditions, principally pollen irradiation. On the other hand, seed irradiation in peanuts has resulted in the mutation of induced mutants back to normal, and in cereals has produced dominant resistance to rust. The evidence from higher plants represents only part of the story. In *Neurospora* many induced mutant loci can be altered back to normal or sub-normal condition, demonstrating conclusively that whatever the nature of the original mutational change, it is not deficiency in the sense of being irreversible (Giles, 1955).

How does the spectrum of induced mutations

compare with that of spontaneous mutations? In *Drosophila*, where extensive data are available, the radiation-induced mutational events are considered by Muller (1954) to cover the same array of types as occurs spontaneously. In plants, most spontaneous mutations occur too rarely for comparison. Stadler (1940, 1944) observed a different array for natural and x-ray-induced genetic changes affecting maize endosperm loci, but here the comparison was between endosperm mutants induced by treating mature pollen, and those occurring spontaneously prior to or during megasporogenesis. Two different types of cells in different stages of development are therefore involved. Ultraviolet radiation, nevertheless, appeared to induce types similar to those occurring naturally. Yet, the identity of even these variants with spontaneous mutants was questioned (Stadler and Roman, 1943; Stadler, 1954; Swanson and Stadler, 1955). MacKey (1954) has shown that the frequency of speltoid mutation may be greater in non-irradiated hybrid material than in progenies from irradiated non-hybrid seeds. In this case the irradiated lot represented the average array of types found in selfed and hybrid material. This would seem to support the view that the agents and time of occurrence for spontaneous mutation are probably of such variety that somewhat different mutation spectra might be found for any two agents or combinations of agents applied. It is thus not unreasonable to expect, as these different experimental results indicate, that only biased interpretations are likely to result if one anticipates that artificial agents should produce a spectrum of mutations equivalent to that observed in nature. In one sense, it might be considered remarkable that the types of radiation-induced mutations are similar to spontaneous types in *Drosophila*. But, even in this case, the spectrum may actually be different in spite of the fact that the same array is found. The differences in mutation spectra indicated from certain experiments greatly justify the optimistic hope that it soon may be possible to willfully guide or direct the mutation of an organism by means of treatment in conjunction with selection.

Are new or previously unknown genetic variants induced by radiations, or are they merely copies of types that occur spontaneously? Whether new or previously unknown mutant types are induced with radiation obviously depends upon the degree of study an organism receives. As mentioned, ionizing radiations appear to produce the same types as occur spontaneously in *Drosophila*. However, Fahmy and Fahmy (1956) have shown that certain chemical agents may mutate loci in *Drosophila* which are apparently stable to x-rays. In their studies of chemical mutagenesis nearly 200 "new" sex-linked recessive visible mutations different both in phenotype and genetic position from those induced by x-rays were recovered. One mutagen in particular, *p*-N-dichloroethyl phenylalanine (a nitrogen mustard derivative), induced 2–3 times the frequency of sex-linked recessive visible mutations, relative to lethal mutations, as any other agent.

In the peanut, where natural variability is somewhat limited, Gregory (1956) has induced a number of apparently new mutant types. In cereals, the range of natural variability has received far more study and few (if any) new characters have been found. However, since little special effort has been made to search for new mutant forms in such plants, one cannot conclude that previously unknown types of variants could not be produced. In fact, if one assumes that radiation or other agents merely increase the frequency of mutation beyond natural rates, previously unknown forms of cereals should be observed only in rare instances.

[An apparently "new" form of stem rust resistance in oats has been recovered recently in a radiation mutation experiment (Konzak, unpublished results). This mutant shows resistance to *Puccinia graminis avenae* race 7a and differs from the single known source of 7a resistance, the Richland factor, in that it is affected by temperature. In this respect the resistance resembles that of the oat variety Canuck which breaks down at high temperature to a number of races but does not cover race 7a. The new form in fact appears to be intermediate between the two types of rust resistance. The genetic identity of the mutant is not yet known.]

What practical or evolutionary significance can be attached to radiation-induced mutations? Let us consider one rather striking illustration. Many investigators might imagine that such lethals as chlorophyll-deficient mutations would be deleterious to plants carrying them in the heterozygous condition. However, Gustafsson (1951) and Gustafsson et al. (1950) have shown that plants heterozygous for certain chlorophyll lethals may express heterosis for a number of characters, including

yield. This type of heterosis could be fixed in asexually propagated plants or in sexually propagated allopolyploid plants. It is known that many cultivated hexaploid oat varieties carry chlorophyll-deficient mutations in one or more homologous pairs of chromosomes (Froier, 1941, 1946). These mutations could not be particularly detrimental to the organism since cultivated varieties have been exposed to severe selection pressures by modern plant breeders. Rather, it would appear that it is because the so-called deleterious genes may restrict or modify certain biochemical processes that they may be responsible in part for the superiority of the strains.

SOME USES OF RADIATION IN GENETIC RESEARCH

The ready production of hereditary changes by radiation has greatly increased our knowledge concerning the genetics of higher plants. Through the study of chromosome breakage, for example, first by direct use of radiation and later by employing special chromosome translocations and rings induced by radiation, McClintock (1931, 1938) confirmed such genetic phenomena as linkage, and determined with reasonable accuracy the relative position of genetic loci on chromosome 9 of maize. The availability of translocations also has permitted Anderson (1956) and others (Burnham, 1956) to speed up chromosome mapping and to extend genetic studies to include loci whose individual effects are not readily distinguished. Still another, but most striking, example of the studies made possible by an abundance of radiation-induced translocations is the recent placing of the seven genetic linkage groups of barley in six of the seven chromosomes by Kramer et al. (1954). More recently, Anderson (1956) and Burnham (1956) have suggested that chromosome translocations may be especially useful for "tagging" genetic factors that are otherwise difficult to identify (such as yield factors) during their transfer from exotic sources to cultivated types where their performance can be measured. Gopinath and Burnham (1956) have demonstrated a method by which reciprocal translocations involving the same chromosomes may be used for producing duplications of genetic loci should they be desired for plant improvement or genetic studies.

Among the most important applications of radiation, however, has been its use for the production of mutations at a great many loci, making possible the ready construction of chromosome maps. Moreover, with this means for speeding up mutation rates, the mutation process itself has been subjected to analysis, and the action and interaction of many genes are already better understood. Mutations affecting such biochemical syntheses as were described in *Neurospora* have been induced in maize (Teas and Anderson, 1951) and *Arabidopsis* by Langridge (1955), confirming further the general similarity of the biochemical processes under genetic control found in lower and higher organisms.

Certain biochemical mutations, for example, those concerned with disease resistance, might conceivably provide more adequate materials for studies on the nature of host-parasite relationships in plants. Studies of Keitt and Boone (1956) on mutant and normal strains of *Venturia inaequalis*, a fungus which causes scab on apples, suggest that the ability or inability of a fungus to live on a host may be closely related to the ability of the host to supply a sufficient quantity of, for example, an amino acid needed for growth by the fungus.

The study of genetic associations in higher plants such as that in oats concerned with Victoria blight susceptibility and resistance to crown rust has been greatly facilitated by the use of radiation. The preliminary investigations, still without genetic analysis, have suggested that the physical separation of genetic factors at the Victoria locus may be somewhat greater than was indicated from inheritance studies completed earlier by others. One interpretation, presented recently by Konzak (1955, 1956) is that this locus, once thought to show pleiotropy, may in reality be a complex genetic locus. Evidence for such an hypothesis has been that radiation-induced mutants resistant to Victoria blight have shown a range of reaction types to one culture of crown rust; only types showing complete susceptibility to crown rust would have been recovered were the induced blight resistance caused by deficiency of the genetic locus. Rare mutant types carrying the typical Victoria resistance to crown rust might occur in any case if the induced blight resistance were due to intragenic change.

In barley, Wettstein (1954, 1956) has utilized *erectoides* mutants to study the property of straw stiffness. He has already identified at least 16 different genetic loci with the erectoid characteristic. One locus is inseparably associated with a translocation (Hagberg, 1954).

RADIATION-INDUCED CHROMOSOME BREAKAGE IN PLANT BREEDING

An especially brilliant illustration of the use of the chromosome-breaking ability of radiation may be found in Sears' (1956) use of x-rays to transfer leaf rust resistance from the wild grass species, *Aegilops umbellulata* L., to the common cultivated wheat, *Triticum aestivum* L. An *Aegilops* chromosome carrying the desired locus was first introduced in the wheat variety Chinese by hybridization with a synthetic type having *Aegilops* as one parent. Since the desired resistance gene was located near the centromere and on the same chromosome with loci having undesirable effects on the wheat plant, chromosome addition or substitution lines were not acceptable. Crossing-over would not occur because the chromosome lacked homology. Reciprocal translocations could probably be obtained readily using radiation, but these were found to carry along undesirable factors from *Aegilops*. It was thus necessary to produce an interstitial translocation involving the desired locus. By employing an isochromosome which occurred by misdivision, Sears doubled the opportunity for the induction of the desired chromosome alteration. Spikes of plants carrying the isochromosome were exposed to x-rays just prior to the onset of meiosis. In three experiments, pollen applied to normal plants yielded approximately 6000 seedlings. One plant was found to possess the desired insertion. This transfer was accomplished by a great deal of effort over many years, because the methodology also had to be developed, but it should be noted that the probability for such a transfer to occur spontaneously in nature is practically nil. The experiment demonstrates that radiation may have use as a tool to incorporate desirable traits from distantly related forms into cultivated plants. Osborne and Elliott (1955) and Larter and Elliott (1956), for example, are employing a technique which involves treatment of seed from the hybrid *T. aestivum* L. × *Agropyron elongatum* L. in an effort to transfer desired loci from *Agropyron* species to wheat. Translocations involving the desired chromosome from *Agropyron* and a wheat chromosome already have been obtained. For a further discussion of the possible utilization of induced cytological changes, the reader is referred to a recent paper by Sparrow (1956).

INDUCED MUTATIONS USEFUL FOR THE IMPROVEMENT OF CULTIVATED PLANTS

The possibility for planned refashioning of cultivated plants to make them better suited to modern agricultural requirements—be they nutritional in nature or concerned primarily with adaptations for modern mechanization—now seems more nearly at hand than ever before. The mass of accumulated data on induced useful plant mutations already obtained attests strongly for such a view. The records do not deny that most mutational events induced are useless or destructive. But they do demonstrate conclusively the necessity for more objective approaches to the problems to be faced in developing more effective methods for inducing and analyzing new mutations. The fact that plant diseases still cause an estimated 3 billion dollar yearly loss to farmers in the United States alone (Benson, 1953) is evidence that plant breeders could make worthwhile use of any additional tools which can be efficiently applied.

It is interesting that the first account of radiation-induced progressive mutations in the United States was reported by Horlacher and Killough in 1933. These authors obtained in cotton mutations from a chlorophyll-deficient recessive virescent (yellow, turning green) plant color to normal green and from recessive forked leaf to dominant normal leaf shape following x-ray treatment of seed. About the same time, Delaunay (1934) and Sapehin (1936) in Russia reported short straw and physiological mutants in wheat. However, the first performance data on induced mutants were reported from Sweden for barley by Nilsson-Ehle and Gustafsson (Gustafsson, 1947). German workers also induced a considerable number of promising mutants in barley, and more recently in other crops (Stubbe and Bandlow, 1947; Oltman, 1950; Bandlow, 1951; Kaplan, 1953; Breider and Reichardt, 1955).

Perhaps of special significance was the induction of disease-resistant mutants by Freisleben and Lein (1942) in Germany. These authors described tests by which they isolated barley mutants resistant to powdery mildew and thus demonstrated the potential usefulness of phytopathological techniques for studying induced mutation in higher plants. Since then, a greater number of x-ray induced mildew-resistant barley mutants have been

recovered (Bandlow, l.c.; Hoffmann, 1951). Hansel and Zakovsky (1956) in Austria have reported evidence that mildew resistance may be produced as frequently in barley as lethal albino chlorophyll variants. Since the albinos make up a high proportion of mutants induced by radiations in barley, other physiological mutants might also be expected to occur frequently in radiation-treated material.

Resistance to stem rust caused by *Puccinia graminis avenae* has been induced in oats by Frey (1955), Myers, Ausemus, Koo and Hsu, (1955) and Konzak (1954). In wheat, stem rust resistance has been induced by MacKey (1954) in Sweden, Ausemus and Hsu (l.c.) and by Konzak, Borlaug and Acosta (Konzak, 1956) in Mexico. Resistance to stripe rust caused by *P. glumarum* (Schm.) Eriks. and Henn., which is one of the important wheat diseases in cool moist climates, has been induced by Hoffmann in Germany (personal communication) and by Konzak, Borlaug, Acosta and Gibler (1956) in a cooperative study completed in Mexico. Hoffmann also indicated that he had induced resistance to leaf rust, caused by *Pucicnia rubigo-vera tritici* (Eriks.) Carleton, and greater tolerance to mildew, caused by *Erysiphe graminis tritici* El. Marchal, in wheat with x-rays, and that his rust-resistant mutants possess resistance to several common races of the pathogen. Resistance to rust caused by *Melampsora lini* (Pers.) Lév. has been induced in flax by Flor (cf. Konzak, 1956). Gregory (1956) has obtained resistance in peanuts to *Cercospora* leaf spot which attacks only certain species of legumes, and, in addition, has demonstrated that progress can be made toward the development of resistance to pod rot caused by *Sclerotium*, a fungus which attacks plants in three different families. The success of these experiments is, in large part, due to the use of efficient methods for isolating mutants. Disease-resistant types are rather readily identified, and with pathogens doing the selecting, large numbers of plants can be tested at a nominal expenditure for labor and supplies. An example of the magnitude of problems involved when searching for some kinds of mutants is indicated by the fact that Gregory (cf. Singleton, 1956) utilized as much as 64 acres of land during one season in the process of identifying useful mutations in the peanut.

Many other mutant traits appear to have breeding value One of these is a maternally inherited *gigas* mutant form of peas induced with x-rays by Gelin (1954) in Sweden. This mutant produces a greater yield than normal types. Useful short-strawed mutant types are readily obtained in wheat (Konzak, unpublished; MacKey, 1954; Whitehouse, 1956). Similar mutant types have been obtained in barley by Swedish workers (Gustassson, 1947, 1954), by Whitehouse (1956) in England and by Shebeski and Lawrence (1954) in Canada, in oats by Frey (1955) and in rice (unpublished results of H. M. Beachell, U.S.D.A., A.R.S.). Short-strawed types are of particular interest for the improvement of standing ability (reduction of lodging) in cereal plants grown under conditions of high soil fertility, and for meeting the needs of modern mechanized farming. Oltman (1950) has reported that mutants with better cold hardiness, baking quality, earliness, lateness, or stronger straw were obtained following x-ray treatment of winter wheat. Higher yielding variants have been induced in a number of cereals by Swedish, German and Austrian workers (Froier, 1954; MacKey, 1956; Hansel and Zakovsky, 1956). Mutant soybeans, maturing as much as 23 days earlier than non-mutants for the same variety, have been obtained in Germany by Zacharias (1956). Chaudhuri and Das (1954) and Jacob (1955) in India report higher-yielding mutants in sesame, *Sesamum orientale* L., and taller mutants in the fiber plant, jute, *Corchorus olitorius* L., after x-ray treatments of seed. The tall jute mutants yielded more fiber than other varieties and sometimes attained a height nearly double that of certain normal strains. Jacob noted that some x-rayed progenies of sesame exhibited varying degrees of resistance to the sesame gall fly, suggesting that insect resistance may be found in irradiated material. In this country Gregory (1955) and Frey (1955) have demonstrated increased yielding ability in mutant strains of peanuts and oats, respectively.

Useful mutants or sports have been induced also in horticultural crops. Lewis (1956) in England has obtained self-fertile mutants in sweet cherry, *Prunus avium* L., as well as evidence which suggests that some physiologic effects of radiation on self-sterility factors may be useful in plant breeding (see p. 36 of this paper). In Germany, a number of useful sports, including some with larger or smaller fruit, fewer seeds, better taste, or with greater tolerance to the white pine blister rust fungus, *Cronartium ribicola* F. de Wal, have

been induced in the black currant, *Ribes nigrum* L. (Bauer, 1956). In this country, Richter and Singleton (1955) and more recently Sagawa and Mehlquist (1956) have obtained flower color "sports" in carnations. In apples, Granhall (1954), Bishop (1954) and Zwintscher (1955) have obtained potentially useful fruit color variants. Sparrow (1954) has noted that somatic mutations affecting flower color in a number of plants were induced with x- and gamma radiation. Breider and Reichardt (1955) have reported an interesting variant in cyclamen induced by x-rays, and Sparrow and Sparrow (unpublished) have isolated both leaf shape and flower color variants in the African violet, *Saintpaulia*.

The stability of mutant strains may sometimes become a problem. MacKey (1954, 1956) for example, observed that some mutant strains in oats may be more unstable than normal types. This problem is not insurmountable, however, since it may be necessary only to backcross mutants with parental types to reconstitute desired factors and remove the accompanying undesirable changes induced. Gregory (1956), on the other hand, has shown that the stability and performance of mutant lines can be maintained at high levels.

Relatively few mutation studies have progressed to a point where varieties carrying induced changes have been released for commercial production. In Sweden an x-ray-induced variant, Primex oil mustard, was released in 1950 and Svalöf Regina oil rape in 1953. In addition, a stiffer-strawed mutant barley strain is undergoing final tests and a higher-yielding mutant pea variety, Weibull Sträl, will be released in 1957 (MacKey, 1956). In this country, the Michigan Experimental Station (Down and Anderson, 1956) has released a new bean variety, Sanilac, which obtains its earliness and bush habit from an x-ray-induced dwarf mutant. Coolhaas (1952) reported that a dominant tobacco mutant with bright leaf color, but with fewer leaves than the normal, is being used in Java as an F_1 hybrid. The F_1 hybrid has the bright leaf color as well as the normal number of leaves. In addition, Coolhaas mentions that a *chlorina* (yellowish-green chlorophyll defective) mutant in tobacco has better leaf quality than normal types. This certainly demonstrates that a "defective type" may have special practical value. For a further discussion of beneficial vs. destructive mutations see Gustafsson (1954).

The seemingly inevitable conclusion from the evidence discussed here is that it should be experimentally possible not only to duplicate the sources of variation found in nature, but also to produce useful changes so rare that they have not been previously known. However, this should not be interpreted to mean that the large world collections of natural variations might no longer be needed. Rather, the two sources of useful variations are most likely to complement each other, permitting fuller use of all the genetic material nature has provided.

MODIFYING FACTORS

In some ways it is unfortunate, yet in other ways fortunate, that radiation effects on cells are subject to modification by a great many external and internal factors. It is unfortunate in the sense that the influence of some agents cannot readily be controlled. Perhaps because of unknown modifying factors the results of treatments applied under a given set of conditions are sometimes difficult to repeat. On the other hand, higher proportions of desired effects may be produced following certain manipulations of treatment and conditions. This latter fact is of considerable significance, since more efficient methods must be developed before mutation work can be considered economical enough for many applications by plant breeders. In fact, the gain in efficiency possible with even the relatively crude methods used today is great enough to merit special attention to methods for altering the mutation response. Some of the most important agencies will be discussed briefly here. Among these are the genetic, physiological, chemical and physical factors.

Genotype. (a) Diploids. The induced mutation spectrum of different species and even of different varieties may vary. In flax (*Linum usitatissimum* L.) and *Arabidopsis thaliana* L., *albina* mutants are quite rare or occur comparatively infrequently, whereas morphological or physiological types of mutants are readily found (Hoffman and Zoschke, 1955; Reinholz, 1947; Konzak, unpublished). In barley, *Hordeum vulgare* L., the *albina* class makes up approximately one-half of the total seedling mutants observed, although morphological and physiological variants also are frequent. Smith (1942) reported that radiosensitivity in einkorn wheat, *Triticum monococcum* L., may be genetically controlled, but apparently does not influence the spectrum of seedling mutations induced with x-rays. Gustafsson (1947) however, noted that a

given dose of x-rays induced more mutations in two recently bred barley varieties, Maja and Ymer, than in Golden, an older Swedish line selection. (b) Natural polyploids. In general, the mutation spectrum of polyploids differs from that of related diploids in the same genus. For example, chlorophyll-deficient mutants are frequent and extreme morphological variants occur in such diploids as barley and einkorn wheat; in the hexaploid common wheat, *T. aestivum* L., however, chlorophyll-deficient types are rarely noted and the morphological and physiological mutants are proportionately more frequent and less drastic (MacKey, 1954). This inverse relationship of chlorophyll-deficient mutants to chromosome number is true for the polyploid series in oats, *Avena strigosa* L. (2N), *A. abyssinica* L. (4N), and *A. sativa* L. (6N), but in the hexoploid species these mutants are observed more frequently than in wheat (Stadler, 1929; Froier, 1946; Konzak, unpublished). Varietal differences in mutation response also occur on the polyploid level, as has been indicated from studies in oats by MacKey (1954), Frey (1955) and Konzak (1956).

Stage of nuclear cycle. The radiosensitivity of cells at various stages of division may differ, and meiotic cells are more sensitive to radiation than mitotic cells (Marshak, 1939; Sax and Swanson, 1941; Rick, 1943; Bishop, 1950; Sparrow, 1951; McLeish, 1955). Sparrow, for example, noted that the radiosensitivity of cells at different stages of meiosis differed rather widely. The most sensitive stage, based on cytologically observed chromosome aberrations, was early diplotene. Singleton and Caspar (1954) (see also Singleton et al., 1956) observed a similar phenomenon for mutation of endosperm loci in maize by gamma radiation. In their study the stage of treatment producing the most endosperm mutations was not the stage found most sensitive to chromosome breakage in Sparrow's experiments, but instead was a stage later and nearer to pollen grain formation. One probable basis for the difference in results is that chromosome alterations induced during more radiosensitive stages may fail to get through later cell divisions. The nature and consequences of alterations induced at the different stages may also differ, however. Lewis (1956) has noted that stable self-fertile mutants in the sweet cherry were obtained only when microsporocytes were irradiated during the "resting" stage prior to the first meiotic division. Irradiation at later stages permitted even greater numbers of pollen tubes to penetrate the incompatibility barrier, but the resulting progenies were all self-sterile and carried the non-mutated alleles. These "revertible" mutants (terminology of Lewis) occurred commonly in non-irradiated controls as well as in irradiated material of clover (Pandey, 1956) and *Oenothera* (Lewis, 1954). It may be argued, however, that "revertible" mutants are not gene mutants at all, but represent physiologic changes in the inhibitory substance (J. L. Brewbaker, personal communication). Perhaps the self-sterility substance may be sufficiently radiation-labile that late treatments may be useful in the production of selfed progeny in systems where it is otherwise most difficult, as in highly self-sterile plants. In this way, inbreds homozygous for sterility alleles could be recovered, then selected and inter-crossed in isolation for the production of single- and double-cross hybrids.

The results of a recent mutation study in *Drosophila*, based on cytological records of the meiotic stages irradiated, merit special mention here. In this study King (1956) found that dominant lethals were induced at high frequencies if female flies were x-irradiated during later stages of egg development; these lethals were totally absent from treatments of very early meiotic stages. However, in striking contrast, recessive lethal mutations were induced at about the same frequency regardless of the meiotic stages in which cells were exposed. This observation suggests that gross chromosomal aberrations (which are no doubt responsible for dominant lethals) may be reduced by treatment of cells during the early or "synthesizing" stages of meiosis or mitosis. It is of interest also to note that the most successful results in plants (in terms of useful mutations induced) have come from studies in which dormant seed, not mature pollen, was irradiated. This striking influence of cell condition may help to explain the negative results of Stadler (1944) in his search for induced dominant mutations in maize.

Water content or physiologic state. The moisture content of the cell is important in the radiation response of plants. It has long been known (Petri, 1921) that the radiosensitivity of dormant seeds was in some way related to their water content. Numerous experiments conducted thereafter further elucidated the phenomenon, but only recently was it established (Caldecott, 1955a, b; Ehrenberg, 1955; Konzak, 1955; MacKey and Konzak, unpub.) that one of the major effects of moisture on the cell system is to modify the radiation response

through its role in cell physiology. Other effects may be closely related to its role as a medium for the transfer of active chemical substances produced in the cell by radiation. One of the oversights of many earlier workers was their failure to recognize that the embryo of the seed alone, or at least principally, is responsive to the radiation, and that seed water content and embryo water content might differ significantly. MacKey and Konzak (unpub.) have obtained data which show that the embryos of dry dormant seeds will absorb most of the water needed to start growth processes after little more than an hour's exposure to water. Yet in this period radiosensitivity is not increased; rather, it is decreased. Since the embryo is only a very small fraction of the seed, water content measurements involving the slower hydrating endosperm do not demonstrate the extremely rapid water uptake. It has been noted also by Caldecott (1955a, b) that dormant barley seeds x-irradiated immediately after storage at 0% relative humidity (R.H.) apparently were more radiosensitive than seeds stored over 32% R.H. or 75% R.H. Thus evidence was obtained for an inverse relationship of sensitivity and moisture content. Seeds stored at 98% R.H. were again more sensitive to the radiation. The importance of the role moisture plays in radiosensitivity varies depending on the kind of radiation. It was found, for example, that the sensitivity of seeds to x-rays may vary as much as 16- to 20-fold, depending on physiological factors concerned with moisture content and germination; there is, on the other hand, only about a two-fold change in the sensitivity of similar seeds to thermal neutrons (Konzak, 1955; MacKey and Konzak, unpub.). The frequency of mutations is greater and the spectrum different when moist rather than dry seeds are exposed to the same dose of x-rays. However, the *highest total* mutation frequency has been obtained from the application of high radiation doses to seeds in their more radioresistant dormant condition (Lutkov, 1937; Tascher, 1929; Gustafsson, 1947; Ehrenberg, 1955). It has been suggested that this happens because the physiological effects of radiation, which can cause cell death, are more pronounced in the more sensitive and germinating seeds (MacKey, 1952).

Storage of irradiated seeds. The effect of a given dose of x-rays may increase with storage. This phenomenon has been utilized by Swedish workers to reduce the cost of x-ray treatments for highly radioresistant plant species. Ehrenberg (1955) has reported that the effect was not observed following fast neutron irradiation. The exact nature of the phenomenon is not yet known, but evidence of Nilan (1955) and Adams et al. (1955) suggest that oxygen may play an important role. These workers observed that storage of irradiated seeds in a nitrogen atmosphere reduced the damage occurring during storage; an oxygen atmosphere either enhanced the effect or did not alter it. Storage at low temperature also served to decrease the effect. A possible interpretation suggested by Nilan (1955) is that the delayed effect may be due to the completion in time of latent or potential breaks induced in the chromosomes of the dormant seed. [More recently H. J. Curtis and N. Delihas (unpublished communication) have observed that the phenomenon is also related to water content or physiologic activity of seeds, since very dry dormant seeds (stored 7 days prior to irradiation over P_2O_5, 0% R.H.) show maximum delayed effect following irradiation while more moist dormant seeds (stored 7 days prior to irradiation at 70% R.H.) show little change. Caldecott (unpublished communication) has also obtained similar evidence.]

With the present state of knowledge regarding this delayed effect in irradiated seeds, it would appear that seeds for mutation experiments should be irradiated when in their most radioresistant condition, as when stored over a saturated solution of NH_4Cl and KNO_3 providing about 70% R.H. They are also less subject to the storage phenomenon under these conditions. It might be presumed, on the basis of the evidence available to date, that this delayed effect may include a higher component of physiologic damage and thus place a low upper limit on the total mutation frequency. This appears to be the case at least for actively germinating seeds and for very dry seeds (Ehrenberg et al., 1953; Ehrenberg, 1955). In the germinating seeds a type of "intrasomatic selection" against viability of damaged cells is thought to occur.

Age. Old seeds are apparently more sensitive to radiation and produce more mutations as well as a different proportion of certain mutations than freshly harvested seeds (Nilan, 1956). As a possible interpretation of this effect, D'Amato and Hoffmann-Ostenof (1956) suggest that the chemical substances accumulated as respiration by-products also may be important in the spontaneous mutation response of dormant seeds.

Nutrition. Stubbe and Döring (1938) have noted that a deficiency for sulfate (SO_4), nitrate (NO_3), and phosphate (PO_4) increased the spontaneous mutation frequency in *Antirrhinum*. In addition phosphate deficiency caused an enhanced mutability response to x-radiation. Seeds from barley plants grown on a medium low in calcium have been shown to be more sensitive to radiation damage than normal seeds (Phillips, unpublished communication). This observation confirms the report by Steffensen (1957) of increased radiosensitivity of calcium-deficient meiotic cells in *Tradescantia*. The chemical composition of plant materials, whether they are grown on deficient or fertile soils, or whether they are infused with such salts as calcium nitrate, cadmium chloride, lithium chloride and sodium chloride, may greatly influence the response especially to thermal neutron radiation (Burdick, see Shapiro, 1956). Boron enrichment of tissue, for example, has been shown to increase the effectiveness of a thermal neutron exposure (Conger, 1953).

Chemical treatments. Colchicine pretreatment will modify the spectrum of induced mutations (D'Amato and Gustafsson, 1948; Gustafsson and Nybom, 1949). Such chemicals as glutathione, cysteine or ascorbic acid are known to confer protection against radiation damage (Mikaelsen, 1954; Riley, 1955), but their effects on the mutation process in plants have received little study. As tissues of different plants may vary in their content of such substances as ascorbic acid, it may be that these are in part responsible for differences in the sensitivity of some plant varieties or species. Chemical pretreatments or posttreatments may be of such importance as to make the use of combined mutagen treatments mandatory for the isolation of mutants from some plants. Other combinations may offer real possibilities for directing the mutation process. The differential action of mutagens in *Neurospora* is well illustrated by the back-mutation studies of Kølmark (1953) and by the mutation and cytogenetic studies in *Drosophila* by Fahmy and Fahmy (1956).

Combined radiation treatments. Pre- or post-treatments combining such radiations as infrared or ultraviolet light with ionizing types have not been tested for their effects on mutation in higher plants. Infrared radiation treatment, while not mutagenic by itself, has been shown to increase the total frequency of x-ray mutations in the fungus, *Aspergillus* (Swanson, 1952). In *Tradescantia*, Yost (1952) has found that infrared post-treatment will nearly double the frequency of x-ray-induced chromosome aberrations.

Swanson (1948) also demonstrated that pre- or post-treatment with ultraviolet light will reduce the amount of chromosomal damage induced by x-rays in *Tradescantia*; in *Aspergillus* combined ultraviolet and x-ray doses induced more mutations than the sum for the two radiation treatments applied separately.

Kind of radiation. The several kinds of radiations are sufficiently different physically that one might expect them to act differently on biological materials. It now has been firmly established that they do act differently for certain measured effects, while they act similarly for others. Further, the results obtained indicate that these effects are quite predictably related to their physical properties. The ion density pattern of a radiation is perhaps one of the most important. For most plant materials, three classes of radiations seem definable in terms of ion density: ultraviolet light is a non-ionizing type; electrons or beta rays, gamma rays, and x-rays are sparsely ionizing; thermal neutrons, fast neutrons, protons and alpha particles are densely ionizing types with a greater linear energy transfer per unit length of track (Zirkle, 1954; Ehrenberg and Nybom, 1954). The influence of ion density on the mutation process may be illustrated by the evidence obtained by Swedish workers that the maximum recovered mutation frequency from treatments of cereal seeds may be 50 to 100 times greater with neutrons than with x-rays (Ehrenberg et al., 1952). Caldecott (1955) observed, however, that when compared on the basis of frequency of interchanges, as many mutations are induced with x-rays as with neutrons. One reason for the apparent difference in results with a single species may lie in the fact that more uniform, and also more consistently predictable, responses can be obtained with neutrons since most of the factors shown to modify the effects of x-rays show less effect with neutrons. The more localized, dense paths of ionizations produced in tissue by neutron irradiation are thought to cause less physiological damage than the more randomly scattered ionization tracks produced by x-rays. Data supporting this contention have been presented by MacKey (1954). He observed that a higher level of transmissible genetic damage was induced by neutrons than by x-rays in polyploid wheat than

in diploid barley. The greater genetic buffering of the polyploid (due to homologous chromosomes) compared with the diploid would, it was argued, permit greater genetic but not greater physiologic damage in the polyploid.

It is well to note, however, that the efficiency of mutation production may be increased by greater ion density only if dense rather than sparse ions are necessary. Energy may be wasted if the amount provided is either too much or too little per unit area to produce an effect. Hence, when compared on the basis of energy dissipated in the tissue volume, it has been observed that densely ionizing radiations may be less instead of more effective in some organisms than in others (Lea, 1946; Stapleton and Hollaender, 1952).

The relative efficiency of the different radiations for producing beneficial mutants is not yet known. Barley seedling data of Caldecott et al. (1954) show no significant differences in the mutation spectra for thermal neutrons and x-rays, although Swedish work with the same crop indicates that some differences may be found for fast neutron irradiation (MacKey, 1952; Gustafsson, 1954). In any cases, approximately the same array of mutant types is produced by each of the ionizing radiations. From tests on mutants and chromosome translocation lines, Nybom (1954, 1956), for example, observed no difference between types induced by x-rays and those induced by neutrons. Thus, there seems to be little cause or justification to use one kind of ionizing radiation in preference to another except for other reasons, e.g., availability of source. In this regard, it is appropriate to note that the effects of thermal neutrons seem to be influenced by fewer modifying factors than other sources, with the result that more predictable data can be attained. This dependability of neutron radiations may justify their greater use in plant mutation studies, since the cost of the labor involved in isolating induced changes far outweighs that of treatment.

Little can be said about the value of ultraviolet radiation as a mutagen in higher plants. Its low penetrating ability restricts its application to mature pollen. With pollens of diploid maize and barley, "physiologic" damage may be so pronounced that very high mutation frequencies appear not to be obtainable (Konzak, unpublished results). So far as known, no mutants of economic interest have been obtained in higher plants with ultraviolet radiation, but these studies were too limited to permit an adequate evaluation.

Radiation dose rate. Critical data on the influence of acute vs. chronic radiation exposures on induced useful mutations are lacking, yet the possibility that low dosage rates may allow an accumulation of genetic effects, but permit recovery from physiologic damage in slowly metabolizing cells, looms as a real possibility. Studies on vegetatively propagated plants in which different dose rates are being compared are in progress at the Brookhaven National Laboratory (Shapiro, 1956). Experiments to test the importance of this phenomenon on seeds should, however, take into account the influence of the "storage" effect as well as that of the moisture content.

Seedling mutation experiments using chronic gamma radiation on growing barley plants have been reported by Nybom et al. (1956). Their results have not indicated any particular gain in efficiency or change in mutation types from the application of radiation in this manner. Similar results have also been obtained by Konzak (unpublished). In actively growing material such as the meiotic or mitotic cells of *Tradescantia*, the chromosome aberration frequency is reduced by a lowering of the dose rate or by dose fractionation (see Sax, 1951; Sparrow and Singleton, 1953). How such results may apply to experiments directed toward the production of useful mutations is not yet known.

Temperature. Treatment with very low or very high sublethal temperatures seems to have an influence on radiation-induced genetic events. As indicated by Stadler (1931), Kaplan (1947), Nybom et al. (1953), and Nilan (1954), freezing of dormant seeds at dry ice (−80°C.) or liquid air (−190°C.) temperatures may reduce the cytologically observable damage but increase the number of mutations isolated. Caldecott and Smith (1952) report that heat treatments at a temperature of 80°C. for ½ hour prior to or following x-irradiation may decrease the frequency of chromosome aberrations as much as 50 per cent but at the same time increase the number of mutations induced by as much as 30 to 50 per cent. This evidence bears on the matter of the efficiency with which mutations may be produced. Further studies would be desirable in order to evaluate the use of x-ray exposure followed by heat treatment for producing useful mutations.

Atmosphere. Exposure of seeds or other plant

parts in the absence of oxygen (e.g., in nitrogen or helium, or in a vacuum) reduces the effect produced by a given dose of x-rays (Hayden and Smith, 1949; Nilan, 1954). This phenomenon is further associated with physiologic activity, since Caldecott (1955) has shown that very dry dormant seeds do not show the marked "oxygen effect." Also, the amount of "oxygen effect" is influenced by the ionization density of the radiation administered. Little response is observed with densely ionizing forms (Giles et al., 1952; Ehrenberg, 1955). From the standpoint of maximum mutation production, the "oxygen effect" must be considered (for the present at least) as having negative value. But it is safe to state, however, that the exact nature of the influence of atmosphere on radiation effects is not yet sufficiently understood, and certain applications might still prove useful.

While this list undoubtedly is incomplete, it may serve to present the reader with a sufficient impression of the numerous paths now showing promise toward the development of better mutation methods. The interested reader should also consider the comprehensive discussions of modifying factors prepared by Sparrow (1951), Sparrow and Forro (1953), Gray (1955), Mortimer and Beam (1955), and Nilan (1956).

CONCLUDING REMARKS

In accordance with a modern concept of mutation types, such cytological changes as deficiencies, duplications, inversions, or translocations—if resulting in a detectable hereditary change in the morphology or physiology of the organism—must be classified as mutations along with those where no such chromosome structural alteration can be discerned. The term chromosome alteration might be retained for the mere rearrangement of chromosome material, if accompanied by no detectable genetic consequence, but there seems little justification for calling one kind of change genic and another extragenic. Even the most subtle chemical change in the genetic material must involve similar phenomena, i.e., the addition, substitution, translocation, inversion, or removal of atoms or molecules.

Hence, such different philosophies of genetics as expressed by Stadler, on the one hand, who maintained the classical concept of the gene as a discrete particle, and Goldschmidt on the other, who developed a view of genetic substance based on position effect phenomena, are in reality not incompatible. Rather, the evidence concerning the nature of mutations seems to confirm the view that mutations are not due to a single phenomenon, but to a series of often quite diverse phenomena.

The gene is no longer imagined in the classical interpretation as the smallest unit of heredity. It may now be subdivided into smaller functional units in higher plants as well as in the lower organisms, phage and bacteria. Yet, a gene is a very convenient unit for describing an hereditary function associated with a locus or segment of a chromosome.

A greater understanding of the fundamental processes of chromosome breakage and mutation, as well as refinements in techniques for altering the spectrum of induced effects and for isolating desirable variants will increase the usefulness of mutagenic agents in genetics and plant breeding. The encouraging results already obtained in the field of mutation research are only an indication of the potential yet to be exploited. However, these agents cannot be expected to replace other established methods and procedures currently used in breeding plants. Instead, their greatest potential value seems to be for speeding up the breeding work in desirable crop varieties without upsetting the arrangement of good qualities, or for producing variability to use in breeding plants where variability is limited, unknown, or difficult to use. Induced mutation methods should be regarded as adjuncts to already proved conventional methods, not as substitutes.

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IV. THE EFFECTS OF IONIZING RADIATION ON PLANTS: MORPHOLOGICAL EFFECTS

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INTRODUCTION

MODIFICATIONS in the growth and development of roots, stems, leaves and flowers in higher plants have been induced by acute doses of x-, γ-, and β-rays and thermal neutrons, or by chronic exposure to γ-rays from cobalt-60. At different dose rates, and depending upon the species or variety used and its age, physiological condition, and radiosensitivity, the response of a particular plant or plant part may be death, growth inhibition, morphogenetic abnormalities, or cellular proliferation. Many of these responses have been reported previously for acute x-ray dosages (Johnson, 1936) and for chronic gamma irradiation (Gunckel et al., 1953a, b; Gunckel and Sparrow, 1954), and there have been several review articles on this subject (Johnson, 1936; Breslavets, 1946; Tolbert and Pearson, 1952; Gunckel and Sparrow, 1954; Sparrow and Gunckel, 1956a).

In order to view the morphological responses of plants to ionizing radiation in the proper perspective, a few generalized remarks are in order. First, the results from one species or variety should not be applied to others, as different types of responses are to be expected in different plants, or even in different stages of development in the same plant (Johnson, 1928, 1948; Sparrow and Singleton, 1953; Sparrow and Christensen, 1953; Gunckel and Sparrow, 1954; Sparrow and Gunckel, 1956a). Secondly, while many responses are abnormal, the observations are not new and may be found in any teratology (Masters, 1869; Worsdell, 1915). Radiation, then, may speed up and accentuate events that are known in nature. This, in turn, means that radiation may be a valuable tool for developmental analysis, particularly where many events in growth are obscured or not observed because of a time factor. Finally, the morphogenetic responses which will be described briefly and, in part, illustrated herein, are the phenotypic expression of genetic, cytological, and physiological factors described in the preceding papers of this symposium and, therefore, capable of analysis and possible explanation.

MERISTEMS

Although the role of meristems in growth, including cell division and cell enlargement, is well recognized, little is understood of their controlling mechanisms. Since very little work has been reported on the histological and cytological effects of radiation upon meristems, they will be considered here first, since their response is fundamental to any morphogenetic processes modified by radiation. Two broad, alternative possibilities concerning the radiosensitivity of meristems are presented in the literature. First, beginning with Bergonie and Tribondeau (1906) and up to the present time (e.g., Nybom, 1956), a considerable number of papers indicated that meristematic cells are more susceptible to radiation damage than "resting" cells. Secondly, as suggested by Henshaw and Francis (1935), there is the possibility that during growth various internal systems or cell components are more easily modified than others. Since the two views are not incompatible or mutually exclusive, each will be examined further in the light of reported research.

Both chromosomal damage and mitotic inhibition may contribute to reduced growth (Sparrow et al., 1952). The most inclusive and consistent work on this has been done on x-rayed root tips of *Vicia faba*. A number of workers (Widoger and Patten, 1929; Jüngling and Langendorf, 1930; Smith and Kersten, 1941) found inhibition of the mitotic process increasing with increasing radiation dosages. This is pertinent in regeneration following radiation damage since the reduction in

rate of growth could be explained as differential killing of meristematic cells due to genetic injury. Those cells most damaged would produce only a few cell progenies so that recurrence of growth would be from cells least damaged genetically (Lea, 1947; Catcheside, 1948; Gray and Read, 1950; Gray and Scholes, 1951; Thoday, 1951; Blume et al., 1950; Mackie et al., 1952; Hagberg and Nybom, 1954). On the other hand, Quastler et al. (1952), working on roots of mung beans, concluded that growth inhibition was not due solely and directly to radiation effects on mitosis but also to induced physiological changes. Working with tobacco, we have found recently that radiation-induced, abnormal, morphogenetic responses are not directly related to the chromosome number or to the number of chromosomal aberrations alone (Meiselman, 1956). Ball (1953) found that when sublethal amounts of both P^{32} and S^{35} were used in a callus culture containing actively dividing cells, certain vacuolated, internal parenchyma cells, even though in division, were more resistant than cells in the marginal meristem. This response might be due to induced changes in the cells or to an oxygen differential (e.g., Conger and Fairchild, 1952). Bloom (1947) reported for animals that mitosis is not a predisposing factor toward radiation damage. We may conclude, therefore, that not all dividing cells are radiosensitive. Further, the specific sensitivity of the chromosomes is not the only primary radiation response and induced physiological changes in both dividing and non-dividing cells must also be considered. Henshaw and Francis (1933, 1935) found a correlation between radiosensitivity and the presence of cells in mitosis. However, since they found it possible to alter growth rate without altering radiosensitivity, it appeared that both growth activity and radiosensitivity were dependent upon a common physiological condition in the organism.

A definite chemical pattern for growth, at least in root tips, has been established (Brumfield, 1942; Goodwin and Stepka, 1945; Erickson and Goddard, 1951; Baldovinos, 1953). The developmental pattern in the so-called apical meristem goes from actively dividing cells, uniform in size and protein content, to actively dividing cells with considerable protein synthesis and moderate hydration, to elongation without cell division accompanied by slight hydration and a considerable increase in protein nitrogen and ash, and, finally, to completion of growth with a rapid increase in the hydration ratio and in carbohydrates but a loss in total protein and ash. With such physiological variability, it would not be surprising to find different "meristem" cells reacting differently to various levels of ionizing radiation. Also, it has been suggested that the effects induced by chronic gamma radiation are more likely to be physiological changes at sublethal dosages rather than irreversible genetic effects (Sparrow, 1951). Friedman et al. (1955) reported that irradiation and chemotherapeutic agents in rats inhibit both cell division and cytoplasmic synthesis. Quastler et al. (1952), Russell and Martin (1952), and Gunckel and Sparrow (1954) presented evidence that physiological (non-mitotic) effects are involved in the response of plants to ionizing radiation. The effects of age on the meristems of *Secale cereale* (Nawaschin and Gerassimowa, 1936) were comparable to radiation-induced changes. D'Amato and Hoffman-Ostenhof (1956) made a very strong case for the death of irradiated cells by toxic substances formed by the chemical action of irradiation, as outlined by Dr. Gordon in a previous paper in this symposium, rather than to mutation or chromosomal aberrations (deletions and ring or dicentric chromosomes) as described by Drs. Konzak and Sax in previous papers in this symposium.

We have little specific information about physiological and metabolic disturbances following irradiation. A relatively high rate of protein synthesis, as outlined above for root meristem cells, may be considered as a characteristic physiological process of cell division. Inhibition of DNA synthesis in irradiated roots of *Vicia faba* has been reported (Pelc and Howard, 1952; Patt, 1954; Smellie, 1953). Cell division is dependent upon the presence of auxins such as indole-acetic acid (Gautheret, 1947). Auxin production is related to metabolic activity and perhaps specifically to protein synthesis (Maskell and Mason, 1930; Avery et al., 1937; Chao and Loomis, 1947), or, in general, where there is active growth there is auxin production (Gunckel and Thimann, 1949). A number of investigators have indicated reduction in auxin levels following irradiation (Skoog, 1935; Smith and Kersten, 1942; Quastler and Baer, 1950; Gordon, 1954, 1956). Loomis (1938) theorized that a mass of dividing cells tended to perpetuate autonomous division so that the cell mass maintained an adequate relative production and

loss of auxin essential to cell division. On the other hand, diffuse meristems such as cambium, slow-growing proliferating tissues or floral apices, and vacuolated tissues were dependent upon external supplies of growth-promoting materials (Loomis, 1938; Snow, 1933, 1935). This theory of Loomis' was substantiated by Ball (1952) in cultures of successive segments from the shoot tip of lupine plants. Further evidence may be inferred from our experiments. Thus, in an irradiated, haploid tomato plant, the meristem of a floral apex was highly sensitive to radiation. On the other hand, the vegetative apex on a similar irradiated plant was relatively unaffected. That is, the apical meristem was intact whereas the highly vacuolated derivatives in the pith were severely damaged (Gunckel and Sparrow, 1954). This response seems entirely reasonable if we consider that cells normally contain protective materials against radiation damage (Mikaelsen, 1952; Cooke, 1953), but floral meristems differ from the growth of vegetative buds in being less able to compete for growth materials (Loomis, 1953a). As a general effect, it might also be added that growth inhibition following irradiation has been attributed to inability of cells to utilize materials available (Quastler and Baer, 1950; Riley, 1953).

Sinnott (1953) clearly stated the fact that morphogenesis represents a series of correlative phenomena—nutritive, compensatory, stimulatory, and inhibitory. Loomis (1953b) considered that the responses of plants to environmental factors, other than the photoperiod or perhaps temperature, could be explained on a growth-differentiation balance—high carbohydrates favoring differentiation and high nitrogen and water favoring growth. To emphasize the need for balanced growth conditions, Loomis (1932) was able to divide the development of a fruiting plant into a regular succession of carefully balanced, alternating, growth and differentiation processes. Skoog and Tsui (1951) were able to show that the balance of growth substances rather than the presence or absence of specific factors controlled morphogenetic responses.

In conclusion, the evidence presented above is clearly contradictory. Subject to further work in this area, and with the exception of clearly demonstrated mutations, or chromosome breakage and aberration, most of the irradiation effects on plant organs to be described herein are to be considered as probably secondary effects of induced biochemical or physiological disturbances.

GROWTH HABIT RESPONSES

Acute and chronic exposures to ionizing radiation have shown that plants are commonly stunted as a result of irradiation, although not entirely so or without regard to dose rates. In general, growth is inversely proportional to the dose rate (or total dose) above a variable threshold level, depending upon the plant, for growth inhibition.

Johnson (1936), in a comprehensive review, reported that most investigators found injury or growth inhibition following x-ray treatments. In our work, this has been figured for shoot growth from potato tubers, tomatoes, tobacco, etc. (Gunckel and Sparrow, 1954; Sparrow and Gunckel, 1956a). Growth stimulation in the x-ray literature is somewhat controversial (Johnson, 1936). It has recently been reviewed by Sax (1955), who suggested that a few successful cases of growth stimulation by x-irradiation indicated that further work should be done in this area.

Chronic exposures of various plants, usually to gamma rays from cobalt-60, have produced essentially the same results as x-rays, again with some notable exceptions. Over 110 species of plants have been investigated for tolerance levels (Sparrow, 1955; Sparrow and Gunckel, 1956a) and most show a general decrease in plant height with increase in dosage levels. Photographic evidence for this has been shown for such plants as *Tradescantia paludosa* (Gunckel et al., 1953a), *Impatiens sultanii* and *Nicotiana rustica* (Gunckel and Sparrow, 1954), *Vicia faba* and *Nicotiana glauca* × *langsdorffii* (Sparrow and Gunckel, 1956a) and

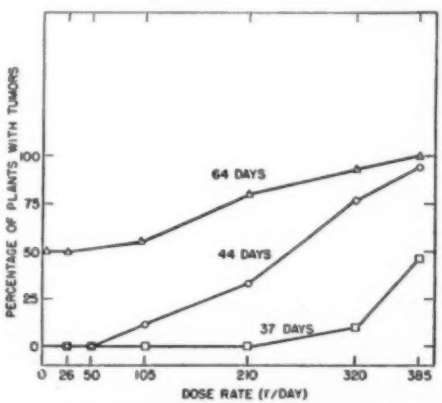

FIG. 1. RELATIONSHIP BETWEEN DOSE RATE AND PERCENTAGE OF TUMOROUS PLANTS AFTER VARIOUS PERIODS OF IRRADIATION

now (Fig. 2) for a composite series on *Nicotiana glauca* from the 1956 gamma field at Brookhaven. Special attention will be directed here to irradiated snapdragons. A detailed study of stem development in irradiated plants of *Antirrhinum majus* var. Yellow Giant was made and showed a decrease in stem height of 0.0084 cm. per r increase in dosage for the vegetative stem and 0.0393 cm. per r for the floral stalk. In the case of flower stalk development an interesting response occurred, mostly at the 175 r per day level but also at higher dosages up to 285 r (Fig. 3). Most plants showed their period of greatest growth during the second to fourth week of irradiation, while some grew at an accelerated rate for three months and to twice the height of normal plants. This seems a clear case of growth stimulation. Other instances are included in the review by Sax (1955).

Any explanation of stem dwarfing is somewhat speculative at this time. Possible explanations might be auxin destruction (Skoog, 1935; Smith and Kersten, 1942; Quastler and Baer, 1950) or inhibition of auxin synthesis (Gordon, 1954 and the preceding paper), the nutritional level (Went and Thimann, 1937, Ch. 5), failure of assimilation mechanisms (Quastler and Baer, 1950; Riley, 1953), or inhibition of mitosis and/or chromosomal damage with associated secondary physiological changes as discussed under the preceding section on "meristems."

Another aspect of growth habit expression lies with the response of axillary buds to radiation. Three species of tobacco will serve as an example. *Nicotiana glauca* control plants have a strongly excurrent stem up until flowering and then axillary buds, just above the middle of the stem, grow out into strong branches. Irradiated plants differ little from controls up to 150 r per day, but above that growth is much reduced. At 200–250 r per day axillaries which grow out at flowering are not restricted to the upper half of the stem. Above 250 r per day apical dominance is lost and axillary branches are as well developed as the leader. Above 300 r per day all growth is inhibited. *N. langsdorffii* normally appears as a small shrub since axillaries keep pace with the terminal. Radiation accentuates axillary branching up to 200 r per day and then growth is sharply inhibited. *N. glauca* × *langsdorffii* grows similarly to the *glauca* parent in having an excurrent stem and regular, restricted, axillary shoots. For several years in gamma field plantings a very low dosage (26 r per day) of gamma radiation has arrested terminal growth and several axillary buds produce strong, equal branches. Increasing dosages decrease height and axillary bud development, with complete inhibition at 250 r. These and similar growth responses in tobacco have been discussed elsewhere (Sparrow et al., 1956).

Another example of modified axillary bud expression resulting in a modified growth habit was described for *Tradescantia paludosa* (Sparrow and Singleton, 1953; Gunckel et al., 1953a, b). In non-irradiated plants, the stem was monopodial to the time of flowering and then sympodial as the upper 3–4 axillary buds developed. At 54–113 r per day, axillary buds opened but were then completely inhibited after 6–8 weeks. After 8 weeks, at 13–37 r per day, multiple, adventitious axillary buds formed irregular leaves on fasciated or multiple shoots in each leaf axil (Fig. 4). These vegetative shoots later formed many aberrant floral stalks. After 12–16 weeks, basal shoots from below ground were initiated in great numbers, especially in the 17–23 r per day range.

Excessive axillary branching of irradiated stems has been reported after fasciation or from growth of radiation-induced buds. This was reviewed by Gunckel and Sparrow (1954).

Any explanation of lateral bud inhibition must rest with the explanation that auxin produced by the apical bud is directly inhibiting (Thimann and Skoog, 1934; Thimann, 1937), or that auxin is not a direct inhibitor but tends to limit in some way the movement of essential materials to the lateral buds (Van Overbeek, 1938), probably because the vascular supply to the axillary buds is poorly developed in their early growth (Moreland, 1934). This problem remains to be investigated further. Skoog (1935) stated that the development of lateral buds was correlated with auxin destruction in irradiated plants. It has been shown previously by Gordon (1954, 1956), and now again in this symposium that the irradiation response is due to the radiosensitivity of auxin biosynthesis rather than to auxin destruction.

EFFECTS ON PLANT ORGANS

The response of a particular plant part may be death, growth inhibition or stimulation, accelerated differentiation, cell proliferation, or morphogenetic abnormalities.

Stems. Common responses of stems to irradiation, in addition to stimulation of dwarfing and excessive branching, include: fasciation, dichotomy, altered phyllotaxis, local stem swellings,

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increase in amount of vascular tissues, and the formation of adventitious meristems or tumors. Since most of these effects were described and figured recently (Gunckel and Sparrow, 1954; Sparrow and Gunckel, 1956a) only a few will be included here.

Stem growth is inhibited in inverse proportion to the dose rate or total dose above a certain threshold value. In order to show, once again, the extent of stem dwarfing, Fig. 5 shows a control plant of *Nicotiana bigelovii* × *N. glauca* on the left and a plant on the right which received 325 r per day for three months.

Fasciation is a fairly common stem response to irradiation, and some plants show this tendency more strongly than others. For example, fasciation has not been observed in thousands of unirradiated snapdragon plants. On the other hand, in the 1953 planting, 4 out of 32 snapdragon plants at 240–350 r per day were fasciated. In a 1952 planting of *Xanthium*, the plants from 125–250 r per day showed well-developed fasciations (Fig. 6).

Localized swellings of stems are fairly common following irradiation. Vegetative stems occasionally show, as in the upper node of a *Nicotiana glauca* × *N. bigelovii* plant shown in Fig. 7, intumescences which are due, in all probability, to a local mobilization of nutrients and auxin. Not uncommonly too, such localized stem swellings are accompanied by the formation of adventitious roots (Fig. 8). In irradiated plants where apical dominance is often lost and axillary buds develop freely, not infrequently the axillary shoots are swollen. An illustration of this in a snapdragon plant is shown in Fig. 9. The shoot on the left is the control and the stem diameter was restricted to about a half centimeter, particularly in this variety where the plant usually consists of several such branches. The branch on the right is much larger, characteristic of single vegetative and floral axes, and is slightly fasciated. In addition, as in this case where the terminal bud failed (arrow), axillary buds which develop late are much larger (up to one centimeter in diameter) because of well-developed vascular connections and the channeling of nutrients into these shoots when the rest of the plant has completed its growth.

Few cases have been reported where radiation treatments increased the amount of vascular tissues produced. In following up a study on the relative responses of n, 2n, 3n, and 4n tomato plants to irradiation (Brody, 1953), it was noted that there is a definite linear trend in differentiation of conducting elements with increasing radiation levels, the xylem increasing with increasing ploidy and the phloem increasing with decreasing ploidy.

Finally, adventitious meristems and tumors

FIG. 2. IRRADIATED PLANTS OF *NICOTIANA GLAUCA* SHOWING THAT GROWTH IS INVERSELY PROPORTIONAL TO THE DOSE RATE ABOVE A THRESHOLD VALUE

These plants were exposed for two months to chronic gamma radiation. The control plant is on the left. The irradiated plants, from left to right, received 200, 250, 325, and 400 r per day.

FIG. 3. GROWTH STIMULATION IN IRRADIATED FLORAL STALKS OF SNAPDRAGON PLANTS

Many plants receiving chronic dosages of gamma radiation of from 175 r per day to 285 r per day responded by prolonged, accelerated growth of the floral stalk, which sometimes reached twice the height of normal plants. The plants illustrated were exposed to 285 r per day.

FIG. 4. MODIFIED AXILLARY BUD EXPRESSION FOLLOWING IRRADIATION OF *TRADESCANTIA PALUDOSA*

This plant received 37 r per day for about three months. It initiated multiple, adventitious, axillary buds which produced irregular leaves and fasciated or multiple shoots. As these shoots grew out, the growth habit was much modified.

FIG. 5. INHIBITION OF VEGETATIVE SHOOT ELONGATION WITH CHRONIC RADIATION

The *Nicotaniana bigelovii* × *N. glauca* plant on the right, receiving 325 r per day of chronic gamma radiation, exhibits severe stem dwarfing as compared to its control on the left. Note also that the irradiated plant formed narrow, strap-like leaves as the lamina of the leaf failed to develop.

FIG. 6. FASCIATION OF AN IRRADIATED *XANTHIUM* STEM

Xanthium plants exposed to chronic dosages of 125–250 r per day exhibited well-developed fasciations such as illustrated in a plant which received 125 r per day for two months.

FIG. 7. STEM SWELLING IN A TOBACCO HYBRID FOLLOWING CHRONIC GAMMA RADIATION

This *Nicotiana bigelovii* × *N. glauca* plant, exposed to 225 r per day, has produced localized stem swellings as inhibited axillary buds form swollen, short-shoots. The leaf bases are also somewhat enlarged.

FIG. 8. STEM SWELLING AND ADVENTITIOUS ROOT PRODUCTION IN AN IRRADIATED *XANTHIUM* STEM

This photograph, taken 29 days following an x-ray dose of 3,000 r, shows the irradiated stem sector at the base which failed to enlarge further. Above the irradiated sector the stem enlarged and a number of adventitious roots formed at the base of the enlarged stem.

FIG. 9. GENERALIZED SWELLING OF AN IRRADIATED SNAPDRAGON STEM

A comparison of the control plant on the left with the one on the right, receiving 285 r per day, demonstrates increased thickness of the irradiated stem. This is often true in axillary branches developed after loss of apical dominance under irradiation. The position of the original terminal bud is indicated by the arrow.

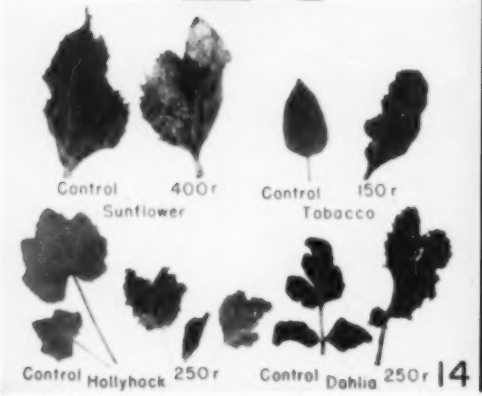

FIG. 10. VARIABLE FLOWERING OF *IMPATIENS* PLANTS FOLLOWING EXPOSURE TO CHRONIC GAMMA RADIATION
The plants in the center and on the right, exposed to 15 and 55 r per day respectively, illustrate increased and/or premature floral production as compared to the control plant on the left. At 15 r per day floral production is premature and increased over the control, while at 55 r per day floral production is decreased in number with decreased axillary branching, but blossoming is premature.

FIG. 11. VEGETATIVE GROWTH IN A NORMALLY FLORAL POSITION FOLLOWING IRRADIATION OF *TRADESCANTIA PALUDOSA*
This plant, exposed to 34 r per day, produced a few sterile flower parts which were succeeded by a number of bracteoles or leaf-like structures. Removed from the gamma field and allowed a recovery period, fused and fasciated vegetative shoots arose from the floral head.

FIG. 12. THE NORMAL FLORAL CONDITION OF *OXALIS*
An unirradiated flower bud of *Oxalis*.

FIG. 13. FLORAL ABNORMALITY OF *OXALIS* FOLLOWING CHRONIC RADIATION
This flower bud, from a plant receiving 625 r per day for several months, has developed a number of bracts or petal-like structures in the normal flower position.

FIG. 14. LEAF ABNORMALITIES RESULTING FROM CHRONIC RADIATION
This photograph illustrates some of the common changes in leaf color, texture, and form. Irradiated leaves often show chlorotic areas, the texture changes as the lamina becomes thickened, puckered, and more pubescent and, most commonly, the leaf blade fails to develop properly so the leaf is irregular in outline.

have been induced on the irradiated stems of *Nicotiana glauca* × *langsdorffii*, with higher dose rates or longer exposure at any one dose rate promoting tumor development (see Fig. 1; Sparrow and Gunckel, 1956b). The increase in number of plants with tumors was accompanied by an increase in the amount of tumor per plant. The probable roles of phytohormones, and of genetic, cytological and physiological factors were recently discussed (Sparrow et al, 1956).

Flowers. In addition to stimulation in height of floral stalks (Fig. 3) and abnormal thickening and fasciation (Fig. 9), irradiated plants may show: delayed and/or reduced flowering, premature and often increased flowering (Fig. 10), color changes and somatic mutations, a high degree of sterility, abscission, modifications in form and number, especially of petals and stamens (Gunckel et al., 1953b), and development of vegetative growths in floral positions (Gunckel et al., 1953a, b; Sparrow and Gunckel, 1956a). Most of these effects were described in the review paper by Gunckel and Sparrow (1954).

One of the most intriguing observations from a physiological point of view concerns vegetative growth in floral positions. An example of this is shown in Fig. 11 for *Tradescantia paludosa*. The shoot terminated in a flower surrounded by four rather than two floral bracts. A few dark, dead and dried, sterile flower parts are seen in the center. These were succeeded by a large number of bracteoles or leaf-like structures and then, during a recovery period from irradiation, a large number of fused and fasciated shoots arose from the flower head. Similarly, an unirradiated flower bud of *Oxalis* is shown in Fig. 12. The flower bud on a plant which received 625 r per day of chronic gamma irradiation for several months (Fig. 13) developed a large number of narrow bracts or petal-like structures in the normal flower position. This indicates that the difference between the vegetative and floral habit is slight, and that the reversion is probably due to the radiosensitivity of a few enzyme systems (see Barron, 1954, and Dale, 1955, for references), or to an induced physiological imbalance (Hagen and Gunckel, unpublished).

Roots. Root growth may be inhibited or stimulated depending upon the dose rate. As mentioned above, the formation of adventitious roots is often associated with localized stem swellings (Fig. 8). In most cases, root growth is inhibited by relatively high dosages, but several plants (e.g., *Helianthus* and *Impatiens*) developed adventitious buds above irradiated stem sectors, presumably due to phloem blockage (Sparrow and Gunckel, 1956a; Gunckel and Sparrow, 1954). The root is a very conservative organ and is reasonably well shielded in the gamma field operation by the soil.

Leaves. The leaves of irradiated plants usually show induced changes in their color, form, and texture (Fig. 14), or even form tumors as a response to local injury. More explicitly, irradiated leaves may show a variety of responses including: mosaic-like color changes or an over-all color change, usually accompanied by increased pubescence; premature abscission; irregular blade development, such as distorted venation, puckering between the veins, abnormal curvatures, fusions, thickening and, most commonly, reduced lamina.

Failure of the leaf blade to develop properly (Figs. 5, 14) is of considerable interest since similar results have been described for unirradiated plants. Of the suggestions offered to account for this effect we have: high concentrations of phytohormones, chromosome fragmentation, mineral deficiencies, and an accumulation of free amino acids (Steinberg, 1956). This problem has been discussed previously (Gunckel and Sparrow, 1954), and several papers are in the process of publication to report our findings on each of these possibilities.

SUMMARY

A brief description of some of the effects of radiation upon the meristems, growth habit, and individual plant organs is given. The responses are diverse and complicated. The morphogenetic effects are interpreted in terms of genetic, cytological, and physiological factors, based upon our work and existing literature on the subject. Most of the morphological irregularities described are probably secondary effects due to physiological imbalances.

ACKNOWLEDGMENTS

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NEW BIOLOGICAL BOOKS

The aim of this department is to give the reader brief yet critical indications of the character, content, and value of new books in all of the various fields of biological interest. Longer reviews will be accorded books of special significance. Authors and publishers of biological books should bear in mind that THE QUARTERLY REVIEW OF BIOLOGY *can notice in this department only such books as come to the office of the editor. The absence of a book, therefore, from the following and subsequent lists only means that we have not received it. All material for notice in this department should be addressed to H. B. Glass, Associate Editor of* THE QUARTERLY REVIEW OF BIOLOGY, *Department of Biology, The Johns Hopkins University, Baltimore 18, Maryland, U. S. A.*

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GENERAL BIOLOGY: PHILOSOPHY AND EDUCATION

THE COMMON SENSE OF THE EXACT SCIENCES. *By William Kingdon Clifford; edited and with a preface by Karl Pearson; newly edited and with an introduction by James R. Newman; preface by Bertrand Russell. Dover Publications, New York.* $1.60 (paper). lxvi + 249 pp.; ill. 1955.

Clifford's *Common Sense of the Exact Sciences* was edited, completed, and first published posthumously by Karl Pearson in 1885. Alfred A. Knopf issued in 1946 a new edition edited by James R. Newman; the present Dover edition is an unabridged and unaltered republication of the latter. It includes Pearson's preface to the first edition, Newman's introduction to the 1946 edition, and a preface to the latter prepared by Bertrand Russell. Enlightening and stimulating as these various commentaries prove, the primary significance of the volume must attach to Clifford's own chapters, which treat number, space, quantity, position, and motion with both originality and exceptional lucidity.

The book was first conceived during a period when mathematics was in a dramatic stage of metamorphosis. It is of value to professional mathematicians, philosophers, and historians in its revivication of the author's role in that movement. It is of equal interest to others less overtly involved in mathematics for the consummate and uncommon clarity with which it presents concepts common to the thinking of every scientist. Both Knopf and Dover are to be thanked for making this inexpensive and eminently readable edition easily accessible to old and new students of science alike.

JANE OPPENHEIMER

THE BIOLOGICAL BASIS OF HUMAN FREEDOM. *By Theodosius Dobzhansky. Columbia University Press, New York.* $2.95. viii + 139 pp. 1956.

This small volume contains a series of related essays by a celebrated geneticist, synthesizing from certain data of biology, cultural anthropology, sociology, and related disciplines a general thesis about the origin, basis, and limits of human freedom. These writings are marked by unusual lucidity of thought and presentation, sometimes also by humor, and often by startling insights and original thought. Along the way, a number of common preconceptions and misconceptions about heredity, environment, race, and culture are challenged (principally on genetic grounds) and, it would appear, are effectively refuted. It is particularly significant that this book comprises the Page-Barbour Lectures for

1954 at the University of Virginia. Given the sociopolitical climate in which they were presented, the book takes on the character of a courageous social document.

The author's careful delineation of the respective possibilities and limits of genetic and environmental influences in the development of the individual human person sets up excellent guideposts for the various disciplines which study man. Dobzhansky makes it quite clear that the assumptions that the human personality is purely biological (genetic) or purely environmental (cultural or psychological) are equally absurd.

Nevertheless, if Dobzhansky is a model of lucidity in dealing with the data of science, he is not always so clear in his handling of philosophical terms. It would be interesting to know precisely what such terms as "good," "evil," "end," "freedom," and "human nature" mean to the author, and this is nowhere made explicit. These are terms which obtain a fixity of meaning (or a denial of any meaning at all) only in the context of some particular philosophy.

The author states that human behavior is ". . . culturally, rather than biologically determined." The question remains whether the existence of what the author admits to being a "non-biological phenomenon in man, culture," or the statement that "Moral rightness and wrongness have meaning only in connection with persons who are free agents," can be reconciled with any sort of determinism. This is a problem with which the author never really comes to grips.

JAMES J. HILL

ON THE NATURE OF MAN. *An Essay in Primitive Philosophy.*

By Dagobert D. Runes. Philosophical Library, New York. $3.00. 105 pp. 1956.

A collection of musings and opinions, half-poetic, and the obvious product of a sophisticated mind rather than a reflection of "primitive philosophy," these essays deal with a few elemental theological notions and a host of the author's prejudices in the fields of history, law, religion, and human progress. The final portion of the book, entitled Evening Thoughts, contains some excellent epigrams as well as three short paragraphs which constitute a most poignant reproach to Christians for their anti-Semitism. Unfortunately, the author has riddled his book with scornful and bitter judgments about all manner of men, but particularly regarding priests and jurists. Runes looks on human nature and human activities with melancholy and sometimes morose pessimism.

JAMES J. HILL

LOGIC AND SCIENTIFIC METHODS. *An Introductory Course. Second Edition.*

By Herbert L. Searles. The Ronald Press Company, New York. $4.25. viii + 378 pp.; ill. 1956.

This introductory college textbook, organized better than most from the pedagogical aspect, and avoiding any radical philosophical position, takes a descriptive rather than critical, historical, or scholarly approach to the problems of logic. The text is rather naive in some places, for example, in the treatment of biological definitions of "genus" and "species."

If the author has avoided the acceptance of any empiricist or positivist extremes, he has also, in discussing such topics as truth and causality, adopted philosophical theses which *preclude the possibility* of a metaphysics—this in an *introductory* text! The opposition of Mill to Hume on the question of causality, rather than, say, of Aristotle to Hume, suggests a narrower scope to the variety of the history of philosophy than is actually the case. The author has, in fact, often stacked the evidence. An enormous lacuna in the history of logic is evinced in this text—a gap between Boethius (d. 524) and Roger Bacon (d. 1626), a period of over 1000 years in the history of logic which the author has chosen to ignore. The model of a scholarly textbook produced by Sir William Hamilton (circa 1850) has perhaps never been emulated.

This second edition of Searles' text represents an elaboration, primarily for pedagogical purposes, of the first edition (*Q.R.B.*, 24: 345. 1949). The bibliography comprises a well-organized selection of basic *modern* texts on logic, scientific method, semantics, and some related disciplines. Nevertheless, this text cannot match, for style, critical spirit, or comprehensiveness, that which was provided by Cohen and Nagel in 1934.

JAMES J. HILL

THE CLASSIFICATION OF LOWER ORGANISMS.

By Herbert Faulkner Copeland. Pacific Books, Palo Alto. $7.50. x + 302 pp. + 1 pl.; text ill. 1956.

The author of this curious book is badly afflicted with a disease prevalent in systematics today—that of raising the ranks of groups. He is not satisfied with anything less than kingdoms and phyla. He has further excavated unfamiliar names for familiar groups. Where such unfamiliar names are actually older this may be justified on ethical grounds, but this practice, if intended, is not consistently followed, e.g., "Flagellata" is older than the adopted "Mastigophora," and "Sporozoa" is older than the strange name "Fungilli" dug out of Haeckel, who in fact seems to be the guiding spirit of the author. One may remark that Haeckel lived some time ago. Raising the ranks of groups implies a lack of a sense of

proportion, an exaggeration of the worth of morphological differences.

The author recognizes four kingdoms, which he calls by the names "Mychota," "Protoctista," "Plantae," "Animalia," in place of the usual Monera, Protista, Metaphyta, and Metazoa. Probably no one will quarrel with him for separating the Monera from other organisms as organisms without formed nuclei—assuming everyone agrees that the bluegreen algae and the bacteria do lack formed nuclei. They do appear to contain chromatin, and some may not regard the absence of a membrane around the chromatin material as of the paramount importance here attributed to it.

The reviewer finds repugnant the concept Protoctista, to which the rest of the book is devoted. Under this name are jumbled together algae other than bluegreens, Protozoa, and Fungi. Protozoa are therefore not considered animals, something no zoologist will accept. There really seems to be no point to this strange mixture, which of course is not new, having been invented by Haeckel under the name Protista—although Haeckel, in fact, excluded organisms with tissues such as the higher fungi. The kingdom Protoctista is divided into 8 phyla, 4 of which are confined to what are generally considered plants and hence fall outside the province of the reviewer as a zoologist. No doubt it is desirable to consider red algae, brown algae, and fungi as separate phyla, and zoologists might even swallow having several groups of flagellates regarded as brown algae. I doubt, however, that they will swallow the separation of the remaining Protozoa into 4 phyla. Most recent books on the Protozoa have only arrived at the grade of subphylum for the main divisions of the Protozoa, previously regarded as classes. The combination of flagellates with rhizopods under the name here of Phylum Protoplasta is no doubt justifiable and appeared in the *Traité de Zoologie*, where its lack of utility was conspicuous. In the present treatise there is much alteration of familiar names. Foraminifera are called "Rhizopoda" and the combination of Heliozoa and Radiolaria, also admissible, is termed "Heliozoa." Not only has the strange name "Fungilli" been dug up from Haeckel as the phylum name for the Sporozoa, but the Ciliophora is raised to the rank of phylum.

The author has undoubtedly spent tremendous labor on this book, and some of his suggestions may eventually find acceptance.

L. H. HYMAN

CELLULAR MECHANISMS IN DIFFERENTIATION AND GROWTH. *Fourteenth Symposium of the Society for the Study of Development and Growth.*

Edited by Dorothea Rudnick; 17 contributors. Princeton University Press, Princeton. $7.50. viii + 236 pp. + 34 pl.; text ill. 1956.

Cellular Mechanisms in Differentiation and Growth includes the eleven papers which were presented in June, 1955, at the Fourteenth Symposium of the Society for the Study of Development and Growth. The first group of communications treats of intracellular events: System Analysis for the Light Growth Reactions of Phycomyces (M. Delbrück and W. Reichardt); The Cytology of Nuclear RNA (H. Swift, L. Rebhun, E. Rasch, and J. Woodard); Plant Cilia and Associated Organelles (I. Manton); and Pattern and Substance in Stentor (Vance Tartar). The second group concerns itself with intercellular relations: Infection and Heredity (J. and E. Lederberg); Cellular Interactions during the Development of the Cellular Slime Molds (M. and R. R. Sussman); New Approaches to the Problem of Embryonic Induction (M. C. Niu); Growth and Development in the Shoot System of Plants (Ralph H. Wetmore); Developmental Correlations in Neurogenesis (Viktor Hamburger); Structural Studies of the Formation of the Myelin Sheath in Peripheral Nerve Fibers (Betty Ben Geren); and Acquired Tolerance of Foreign Cells (R. E. Billingham).

If the separate chapters are, inevitably, somewhat disparate in style and quality of presentation, they are all nonetheless of uniformly high interest in so far as their content is concerned. Embryologists and other investigators concerned with problems of development and growth, in days when most professional societies show such strong tendencies to specialize rather than to generalize themselves, enjoy great advantages as a result of this Society's sponsoring of symposia which repeatedly bring differing points of view to bear on central developmental problems. The Princeton Press performs a unique service for the whole biological reading public by continuing to make available this fine series. Its handsome volumes deserve a place on the shelves of all who interest themselves, to any degree, in the focal problems with which they deal.

JANE OPPENHEIMER

BIOLOGY: HISTORY AND BIOGRAPHY

HUNGRY GENERATIONS. *The Nineteenth-Century Case Against Malthusianism.*

By Harold A. Boner. King's Crown Press, Columbia University, New York; [Columbia University Press, New York]. $3.75. ix + 234 pp. 1955.

Every schoolboy who knows anything about evolution knows that both Darwin and Wallace read the *Essay on Population* by Malthus, and that from this essay came the germ of that idea which eventually grew into the Darwinian theory of evolution. The crucial in-

formation which Darwin derived from Malthus was that the population and the food supply are not always in balance, from which he concluded that an over-abundance of the former coupled with an insufficiency of the latter led to a situation where survival resulted only after struggle and was the reward of the fittest. What is perhaps not so well known is that this conclusion was something that Malthus himself never dreamed of, for the *Essay on Population* was written by a well-to-do Englishman seeking to explain the basis for poverty and the prolificness of the poor. It is with this aspect of the question that Harold Boner deals, and he has therefore attempted to chronicle the rise and fall of Malthusian doctrine in nineteenth-century England.

It is the author's principal contention that the Malthusian doctrine is false at heart, and that for nearly a half-century it was a real obstacle to social progress and reform. Malthus had written his essay in 1798, when one of the big questions facing England was the increasing number of poverty-stricken people and the means for dealing with them. This was a topic which engaged the finest minds of the time, and the *Essay* served to split the thinking population into Malthusians and anti-Malthusians. Malthus maintained that the poor created their own poverty largely because of their own proclivity for large families, by their "imprudence," as Malthus stated it. Any relief of poverty through the medium of "poor laws" would, in the end, only deepen their misery by stimulating their imprudence. Malthus, therefore, was against any form of charity. The anti-Malthusians, on the other hand, considered that the poor were poor because of an inequality in the distribution of the wealth of the land, that poverty is a measure of the disparity between the wealthy and the poor, and that the Malthusian doctrine was a device for the privileged to preserve their favored economic status.

Boner handles his topic very well, and takes the reader through the periods which saw the rise of Malthusianism (1798—1817), its triumphant stage (1817—1834), and its eventual decline (1834—1859). These are, of course, separations made by the author, and the three major dates (1798, 1834, and 1859) coincide, respectively, with the appearance of the *Essay*, Malthus' death, and the publication of Darwin's *Origin of Species*. Boner concludes that by 1859 Malthusian doctrine had ceased to dominate men's minds, but what is not made clear is the fact that at this time the Industrial Revolution had converted the poor from a drug on the market, to be supported and sustained by the state, to a segment of the population sought after to man the machines in the factories of the wealthy. It was a time of industrial expansion, and if the poor could, through imprudence, produce more hands to man more machines, who was to say that it was imprudence, since they were really supporting themselves? However, it takes but a slight turn of economic events to change a population from a producing to a non-producing state, and to change the tenor of men's minds in regard to the poor, and the circumstances prevalent today in India and the Latin-American countries strongly suggest that Malthus knew whereof he spoke.

It is of interest to note that the most enthusiastic denouncers of Malthusian doctrine, even during its triumphant period, were the literary leaders of the age: Hazlitt, Coleridge, Southey, Wordsworth, and Shelley. No scientist of note is mentioned by Boner as having been a powerful opponent of Malthus, and it is probable today that a census of opinion would reveal a similar cleavage between the literary "sociologists" and the natural scientists.

C. P. SWANSON

THE YOUNG NATURALIST

LIFE IN FRESH WATER.

By E. S. Brown. Oxford University Press, New York; Geoffrey Cumberlege, London. $2.75. 64 pp. + 1 pl.; text ill. 1955.

Again the editors of the Oxford Visual Series have produced a book which is so interesting that no young reader or adult beginner can help becoming fascinated with ponds, streams, and marshes and the plants and animals which live on, in, or adjacent to these waters. This is an ideal gift for potential biologists of high-school age. The fact that the book is published in England does not render it less valuable to American naturalists, because the entire subject is treated in such a general manner as to be applicable to this country as well as to lands abroad. *Life in Fresh Water* is truly a delightful book.

V. G. DETHIER

RACES AND PEOPLE.

By William C. Boyd and Isaac Asimov; illustrated by John Bradford. Abelard-Schuman, New York. $2.75. 189 pp.; ill. 1955.

The term "race" has, through the years, been provided with many qualifying adjectives, some damning, others praiseworthy; some loosely applied, others used only in a very restricted sense. Most frequently, however, the term has been given a sociological twist with little knowledge of its true biological meaning, or has been used by demagogues with meaningful perversion for specific purposes. Abuse has therefore been heaped upon the term, and this abuse has, in turn, left misconceptions as to the basis of racial differences and as to the gulfs—physical, biological, psychological, national, etc.—that separate various peoples. The authors have courageously tackled this problem for our young

people, and they have presented a straightforward discussion of racial differences in terms of genetics and evolution. They have rightly stressed the meaning of "frequency" as a key word in the interpretation of any racial trait, and they have given "variation" its proper place and connotation.

In this day of racial tension and bitterness, the hope of our society in eradicating artificial barriers erected for the benefit of one segment of society at the expense of another lies in the young who see things with a less prejudiced eye. This book should help to strengthen their thinking on what has become a touchy subject, and should be required reading for the developing teen-ager. It is perhaps too much to hope that his parents could profit as well.

C. P. SWANSON

ECOLOGY AND NATURAL HISTORY

OBSERVATIONS ON THE FISH POPULATION OF A LAKE CONTAMINATED BY RADIOACTIVE WASTES. *Bull. Amer. Mus. nat. Hist., Vol. 110, Art. 4.*

By Louis A. Krumholz. American Museum of Natural History, New York. $1.50 (paper). Pp. 277-368 + 1 map; ill. 1956.

A strenuous attempt was made to evaluate the effect of radioactive wastes on fish populations in nature. Unfortunately, no studies were done before the wastes were dumped, nor was a comparable lake available during the study. Thus we have, as the title says, "observations" that the fish populations declined during the 3 years, but no real proof of a causal relation. Fortunately the techniques developed and pitfalls sighted will be invaluable for a future controlled study.

DAVID E. DAVIS

DAYS WITH BIRDS. *Studies of Habits of Some East African Species. Fieldiana: Zool., Vol. 38.*

By V. G. L. Van Someren. Chicago Natural History Museum, Chicago. $8.00. ii + 520 pp. + 1 pl.; text ill. 1956.

Over a period of many years' residence in Kenya Colony, V. G. L. van Someren made intensive studies of a large number of species of birds. Using the technique of a "hide" or "blind" set up near the nest, he was able to observe individual case histories at close range over as many consecutive days and even weeks as needed, and he made thousands of photographs. In the present book he limits himself to accounts of 160 species studied in his 40-acre sanctuary at Ngong, near Nairobi. Originally part of a longer manuscript with many more illustrations, the present book was written for more general reading in the hope of stimulating interest in birds, especially among the younger settlers in that area. It was not possible to get the larger work published, and it is fortunate that the Chicago Natural History Museum has brought out the ornithologically most valuable part of the work, as otherwise these detailed first-hand observations might have remained buried in the limbo of unpublished, and, hence unavailable, data.

For numerous species, van Someren's accounts constitute the most extensive and most important single source of information, and his photographs are the first, if not the only, ones of the birds they depict. The observations in some cases are as detailed and intimate as those to be found in the best studies of North American and European species, even if not as complete. However, we must remember that these are all the author's own data; there were none of other observers for him to use to fill in the gaps of his personal accounts.

Austin L. Rand undertook the delicate task of reducing the original manuscript and its illustrations to publishable size, and also saw it through the press. The author had no opportunity to participate in any of the final decisions involved. While van Someren may well feel disappointment at this reduced version of his manuscript, the result is an important contribution to our knowledge of African birds.

HERBERT FRIEDMANN

NATURAL HISTORY OF BIRDS. *A Guide to Ornithology. By Leonard W. Wing. The Ronald Press Company, New York.* $6.75. xi + 539 pp. + 1 pl.; text ill. 1956.

Although less definitely a formal classroom text than some other recent volumes on ornithology, this book is to be looked upon as a textbook rather than a new appraisal of the subject it covers. The author had in mind both enrolled students and free-lance bird watchers, and wrote a book to give them a general coverage of those topics of avian biology normally left out of faunal, systematic studies and identification manuals. In this he has been successful on the whole, although the chapters appear to have been written over a number of years so that some are more up to date than others, and a few read as if somewhat strained by the effort to simplify complex subjects for the general reader.

While the author has drawn from birds of all parts of the world for his discussion, he has used well-known species as much as possible as illustrative examples, a plan that should make the book more easily used by amateur readers. In the same spirit, Wing has kept the text as free as possible of scientific names, and includes a glossary of terms he has used.

The topics discussed are divided into 24 chapters,

each of which closes with a selected bibliography. In addition, there is an extensive literature list at the end of the book. The line drawings used are good and make clear, readily intelligible illustrations; the photographs are not as satisfactory. The book is well indexed and should be a useful guide to amateurs and students of ornithology.

HERBERT FRIEDMANN

PRAIRIE DUCKS. *A Study of Their Behavior, Ecology and Management.*

By Lyle K. Sowls. The Stackpole Company, Harrisburg; Wildlife Management Institute, Washington. $4.75. xiv + 193 pp. + 20 pl.; text ill. 1956.

From 1946 to 1950, Sowls collected data on mallards, pintails, gadwalls, shovellers, and blue-winged teal in the research area at Delta on the south shore of Lake Manitoba. A number of results for these species verify previous conclusions based on scanty information. Adult females (if alive) and some young return to the nesting area of the previous year. The males do not as consistently return, presumably because the birds pair on the wintering grounds and the female dictates the return site. When the birds are in the nesting area, they have a very limited range. The details of nesting and of raising young are described for these five similar species, and some excellent summaries of data on clutch-size, hatching, and mortality are presented. The final chapter carries the ducks to the hunter's gun.

The book is nicely illustrated with photographs, sketches, and graphs, and has a good index and bibliography. A fundamental problem in a book of this type is the presentation of original data. The book is designed for the general biologist and sportsman, and to verify the conclusions often would require much detail. Consider Table 21. The conclusion is that "a decrease in [clutch] size occurs in all species as the season advances." But the table gives only averages and thus, while the data appear consistent with the conclusion, a real check is not available nor are the data yet published in detail elsewhere. The problem of verifying the conclusions will discourage the use of this book for an examination of basic biological principles.

DAVID E. DAVIS

THE SAGA OF THE GREY SEAL. *Introducing the Natural History of the Grey Seal of the North Atlantic.*

By R. M. Lockley. The Devin-Adair Company, New York. $4.00. vii + 149 pp. + 8 pl.; text ill. 1955.

Lockley has a fine and sensitive gift of expression, the patience and watchfulness of the true naturalist, and a flair for the dramatic that tends to envelop common things with an uncommon beauty. He exhibited these traits in his earlier books on birds, and he does so again in this volume which deals with the breeding habits of the Atlantic, or grey, seal along the rugged Welsh coast. From a scientific point of view, Lockley leaves no stone unturned to document fully the breeding habits and family life of the seal, from the time that the adults appear on the beach up to the time that the young seal is sufficiently grown to enter the Atlantic Ocean on its own. In a literary sense, this is a tale that unites the haunting loveliness of the coast with the loneliness of a solitary vigil by the sea.

C. P. SWANSON

THE DEER OF NORTH AMERICA. *The White-tailed, Mule and Black-tailed Deer, Genus Odocoileus. Their History and Management.*

Edited by Walter P. Taylor; editorial committee, Arthur S. Einarsen, Ira N. Gabrielson, C. R. Gutermuth, Aldo Leopold (deceased), and Walter P. Taylor, chairman; color plates by Walter A. Weber; drawings by Wallace Hughes. The Stackpole Company, Harrisburg; The Wildlife Management Institute, Washington. $12.50. xx + 668 pp. + 2 pl.; text ill. 1956.

This comprehensive volume by members of the United States Fish and Wildlife Service and Forest Service, state game administrators, educators, and practical scientists is a contribution of the Wildlife Management Institute. It is directed to hunters, naturalists, wildlife administrators, biologists, and educators. It is the only comprehensive volume treating all aspects of the life history, habits, and management of North American deer. It is a consolidation of all available information. Among the topics discussed are: The Deer, the Indians, and the American Pioneers; What and Where are the Whitetails?; Life and Times of the White-Tailed Deer; Management of the White-Tailed Deer in its Environment; Hunting the Whitetail; What and Where are the Mule and Black-Tailed Deer?; Management of the Mule Deer; Hunting Mule Deer; and Life and Times of the Coast Black-Tailed Deer. The profuse illustrations include full-color plates of the white-tailed deer and the mule deer. The book is replete with statistics. As a reference volume, it contains answers to most of the questions which might be asked concerning deer.

V. G. DETHIER

THE AUSTRALIAN MUSEUM MAGAZINE. *Vol. XII, No. 3.*

Edited by J. W. Evans. The Australian Museum, Sydney, N.S.W. 2s. (paper). ii + 102 pp. + 1 pl.; text ill. 1956.

This journal is in its twelfth volume, and consequently

is not a newcomer in the area of biological literature. However, it is called to the attention of biologists again because the new director of the Australian Museum in Sydney, Dr. John Evans, has recently reorganized, brightened, and enlivened the journal. In its new format it is an attractive and informative museum contribution. Most of the articles deal with the natural history of Australia, but their interest, of course, is not so narrowly restricted.

EVOLUTION

FEATURES OF EVOLUTION IN THE FLOWERING PLANTS. *By Ronald Good; illustrated by Marjorie E. Malins and the author. Longmans, Green & Company, London, New York, Toronto.* $6.00. xv + 405 pp.; ill. 1956.

Ronald Good begins his interesting and stimulating book with a complaint. So far as evolution is concerned, he believes that the major support for the theory has come more from the study of zoology than from that of botany, the reason being that because bones are so much better preserved than plant parts, the reconstruction of past zoological events is on substantially firmer ground. He reasons, therefore, that the tenets of evolutionary thought should be re-examined in the light of current botanical knowledge. This he proceeds to do by comparing plants with animals in the evolutionary features which run parallel or diverge in the two kingdoms; by reviewing the families of flowering plants in terms of their floral structure and suggested affinities; and by examining in detail two advanced, highly developed, and uniform families, the Asclepidaceae and the Compositae. From these comparisons a number of conclusions have been drawn: (1) evolution in both kingdoms is fundamentally the same process; (2) evolution in the green plants is an independent process while that in animals is not necessarily so, since animals are ultimately dependent upon plants for their existence; (3) evolution in the green plants seems to be gratuitous and motiveless, in the sense that the changes which can be detected result from the fact that change is part of the innate order of nature rather than that change confers biological superiority and hence insures its own perpetuation; (4) evolution has been a "process of continuous automatic impetus" which is the antithesis of stagnation and is a characteristic peculiar to protoplasm; (5) evolution has embodied within it an important element of repetition that is expressed in both related and unrelated lineages; (6) evolution, in addition to being motiveless, is also an elaborative process, and this accounts for the great diversity of flowering plants; and (7) the flowering plants are not the result of an evolutionary process which, in the Darwinian sense, is competitive and eliminative, but are rather the result of a type of change which has an expansive instead of a contractile expression.

It is to the last conclusion that most biologists will want to take vigorous exception. Good, in essence, is stating that evolution, as he sees it, cannot be interpreted in the Darwinian sense that natural selection is the sieve through which all organisms must pass, and he suggests that "no matter what new characters or new combinations of old characters change with time may present they are all able to find an existence somewhere in the scheme of things." There is, as a consequence, a pronounced element of the "age and area" theory of J. C. Willis in Professor Good's reasoning, but I believe it would be fair to state that no modern experimental systematists and few descriptive ones find Willis' ideas grounded in fact. It is probably true that all individuals *could* "find an existence somewhere in the scheme of things," but for this to come to pass, the individual and the proper environment must coincide in time and space for survival to occur. In the Darwinian sense, it is just this precise juxtaposition of these two elements which permits natural selection to operate, and which makes evolution the opportunistic and expedient process that it is. The rapidity with which populations shift and change will, of course, depend upon generation time, but the delicateness of the balance between the individual and the environment is indicated by the studies of Dobzhansky and his students on *Drosophila pseudoobscura*, the botanical studies of Edgar Anderson which point to the influence of man as a source of environmental disturbance, and the fine work of experimental taxonomists such as Jens Clausen.

Good has produced a stimulating book, and it is always of interest to consider old problems from other points of view, but few would agree with the author that "the remarkable success of Darwin's theory was undoubtedly due in chief to the fact that the world was ready for it." The thinking world undoubtedly was ready for it, but this fact alone cannot account for its continued persistence despite innumerable challenges and the means for testing, at least in a limited way, its validity. It seems highly unlikely that Darwinism would have permeated biology to the extent that it has, had it not something more to contribute than an immediate, but shallow-rooted, appeal.

C. P. SWANSON

GENETICS AND CYTOLOGY

INTERNATIONAL REVIEW OF CYTOLOGY. *Volume V. Edited by G. H. Bourne and J. F. Danielli. Academic Press, New York.* $11.50. 570 pp.; ill. 1956.

The present volume continues the trend established by earlier volumes of the series, in that cell physiology and cytology are treated as but two aspects of a single

discipline. Form and function are not inextricably mixed as they would be if all were known, but neither are they treated separately. The titles of the several reviews, together with the authors, will provide the best index of the contents of Volume V: Histochemistry with labeled antibody (A. H. Coons); The chemical composition of the bacterial cell wall (C. S. Cummins); Theories of enzyme adaptation in microorganisms (J. Mandelstam); The cytochondria of cardiac and skeletal muscle (J. W. Harman); The mitochondria of the neuron (W. Andrew); The results of cytophotometry in the study of the deoxyribonucleic acid (DNA) content of the nucleus (R. and C. Vendrely); Protoplasmic contractility in relation to gel structure: temperature-pressure experiments on cytokinesis and amoeboid movement (D. Marsland); Intracellular *p*H (P. C. Caldwell); The activity of enzymes in metabolism and transport in the red cell (T. A. J. Prankerd); Uptake and transfer of macromolecules by cells with special reference to growth and development (A. M. Schechtman); Cell secretion: a study of pancreas and salivary glands (L. C. U. Junqueira and G. C. Hirsch); The acrosome reaction (J. C. Dan); Cytology of spermatogenesis (V. Nath); and The ultrastructure of cells as revealed by the electron microscope (F. S. Sjöstrand).

The articles by Harman, Andrew, the Vendrelys, Schechtman, and Sjöstrand seemed particularly good, although all appear to be, with one exception, adequate reviews of subject matter. The one exception is the article by Nath, but the criticism is not that it is inadequate but that it is mistitled. Since it is particularly concerned with the development of the spermatozoid from the spermatid, and with the evolution of the acrosome and the mitochondrial nebenkern, it is more properly concerned with spermiogenesis than with spermatogenesis.

C. P. SWANSON

GENERAL AND SYSTEMATIC BOTANY

BRITISH KNAPWEEDS. *A Study in Synthetic Taxonomy. By E. M. Marsden-Jones and W. B. Turrill. Ray Society, London.* 27s. 6d. xiii + 201 pp. + 27 pl.; ill. 1954.

This is a cytotaxonomic study of three species of Knapweeds or Hardheads native or naturalized in Britain: *Centaurea nigra* and *C. nemoralis*, native, and *C. jacea*, which "has been, and from time to time probably still is, introduced from the Continent . . . . It occurs spasmodically in time and space." Knapweeds resembling *Centaurea scabiosa* occurred in the London area from the late glacial to the boreal period, to judge from pollen grains recovered from the Lea Valley. The Lesser Knapweed (*C. nigra*) *may* have been present in pre-Roman times in Britain, when there was much more woodland than at present on her chalk exposures. The three species studied all have a chromosome number of $2n = 44$ and are completely interfertile. "The analysis of populations of British knapweeds . . . is far from complete. The results can, however, be stated with considerable confidence in the form of a generalization," say the authors. "The marked reticulation of characters found from individual to individual and from population to population is due primarily to hybridization and secondarily to recurrent mutation. Limitations to reticulation are imposed by the selective action of environments in which climatic, edaphic, and biotic factors are all involved."

Problems noticed in wild populations guided the choice of breeding experiments, and herbarium vouchers were preserved of stock plants and of their offspring. Characters of head, floret, and cypsela (or achene) were concentrated upon in their analyses of populations. There is essentially no consideration of the results obtained in America by Clausen, Keck, and Hiesey and their school with such Compositae as the tarweeds and *Achillea*. The authors' attempt was to "demonstrate the methods and some results of synthetic taxonomy," that is, the use of as many kinds of characters and data as possible, "not primarily as either genetics or population analysis." But I think the dedication—perhaps of altruistic intent—an unwarranted jab: "we dedicate what we have accomplished to all who are helping to rejuvenate plant taxonomy."

"Hybrid swarms involving *Centaurea jacea* with the two species, *C. nigra* and *nemoralis*, were detected many times. Phyllary shape was found to be the best index of hybridity," and "can be studied as well in dried as in living material—one is, indeed, tempted to say that the preserved specimens may sometimes be the better." Shades of Asa Gray! And the apochryphal story of his having to press specimens before he could name them! There is sound basis for the authors' declining to name hybrids but designating the known or putative parents, "precised by reference to phyllary structure," as for example, "*Centaurea jacea* x *C. nigra* (and phyllaries S[ome])." "Proving that various so-called species [proposed by C. E. Britton in particular] are abstractions from such hybrid swarms" is one result of the study. Hybrids between *C. jacea* and *nigra* are reported from Oregon and from Del Norte County, California, based on six collections sent by John Thomas Howell. The status of the original introductions into these regions, whether pure species or themselves hybrids, is unknown, and presents an attractive problem. Populations of both species, *sens latus*, are known from eastern United States.

Interesting habitat notes are provided; especially welcome would have been more field notes from the Continent where *Centaurea jacea* grows as a pure species and in hybrid swarms. "[Knapweeds] quickly succumb

to smothering and even suffer from excess of their own top hamper." California botanists stuck with tarweeds might welcome this novel descriptive term for the leafy crown! "Taxogeny" is proposed to replace "phylogeny" because of the duplicating use of "phylum" in the hierarchy of classification, but, like "cell," "ovary," and many another term of faulty connotation, phylogeny has won a permanent place in biological language.

British Knapweeds opens with an attractive frontispiece in color of six different combinations of ray and disc florets to be encountered in the three species, as a sort of "homologous series in variation" (though that useful concept is nowhere used in the book). The best-written chapter of the book is the General Introduction of somewhat less than twelve pages. This chapter provides the gist of the story and might be profitably followed by Chapter Ten, Conclusions. The chapter on the Taxonomic History of British Knapweeds is not easy reading; in fact, a student coming upon this chapter would, to borrow our Negro porter's phrase, be "mighty disencouraged" ever to venture further into plant taxonomy. The words "confused" and "confusion" occur frequently, and order is not improved by the erratic intercalary references. The bulk of the book is given over to lists, tables, paragraphs, and pages of data (often raw) that are published as supporting evidence for the conclusions; all of this would have been better treated as appendices. To open the book at random—take p. 66—the reader is in the midst of a wild knapweed patch where page after page of data, "eradiata normalis," "radiata normalis," "radiata longiflora," following "terms and standards" given in the Preface, stand in weedy monotony. After forcing his way through this top hamper of data the reader emerges with a sentence: "it is interesting to record the occurrence of *C[entaurea] jacea* in 1796 and *C. nigra* in 1846 in the Belfast area and slight traces of *C. jacea* genes in 1952" (p. 79). Sixty-two pages (Chapter Six) devoted to genetical experiments presented some difficulty to the authors, they admit, and they presented the data under five headings. The chapter amounts to an extended appendix for the next chapter, Genetics of Reproductive Parts and Chapter Eight, Compatibility and Incompatibility, both of considerable interest to the cytogeneticist, particularly if he is addicted to the Compositae. But, again, these chapters are cluttered with data that interfere with straightforward contemplative reading. This study, which represents an enormous fund of painstaking fact-gathering, is an unhappy example of poor organization. But this cypsela of a monograph will one day come into full flower in a knapweed experimental plot of the future, against the "changing flora of the British Isles," toward the new systematics. Julian Huxley (1940) was prophetically correct when he said "that such micro-evolutionary studies will become increasingly important in the near future."

JOSEPH EWAN

PLANT PHYSIOLOGY

PLANT PHYSIOLOGY. *Fourth Edition.* *By Meirion Thomas; with the collaboration of S. L. Ranson and J. A. Richardson. Philosophical Library, New York.* $12.00. xii + 692 pp.; ill. 1956.

The first edition of this book in 1935 was one of the early attempts to interpret the physiological processes of green plants in terms of physico-chemical concepts. In the twenty-one years that have elapsed since the first edition, the fields of plant biochemistry and biophysics have developed enormously. In this fourth edition of *Plant Physiology* the author has managed to keep abreast of the new literature and has presented a well-rounded survey of the current status of plant physiology. It is well-nigh impossible for a single person to keep up with the current literature in plant physiology and, in this new edition, Professor Thomas has had the collaboration of two of his colleagues at the University of Durham.

The book is organized in four parts. The first part deals with the activities of protoplasm at the cellular level. Glycolysis and the oxidative catabolism of carbohydrates are covered in modern terms. There is also an excellent discussion on the enzymes and carriers involved in oxidations and reductions. Part Two is concerned with those physiological processes peculiar to plants: the absorption of water and solutes from soil by roots, transpiration, the conduction of water within the plant, the conduction of solutes, and the gaseous exchanges between plants and the outside air. Wherever possible, the discussions are based upon our present knowledge of physics and chemistry. Part Three is a discussion of nutrition and metabolism, including photosynthesis. The photosynthesis section includes most of the new work with radioactive carbon dioxide and the path of carbon. Part Four covers growth and movement. This part of the book has been considerably expanded over previous editions. Throughout all of the book, stress is placed on experimental methods and the interpretation of data. Many illustrations are given of specialized apparatus and equipment.

A useful feature of the book is the inclusion in several appendices of detailed information on the occurrence and chemistry of many of the metabolic products formed in plants. Another appendix contains material on some of the newer techniques of biochemistry: chromatography, ion-exchange and isotopes. Finally, the book contains a good bibliography (748 entries), author index, and subject index.

G. R. NOGGLE

ANNUAL REVIEW OF PLANT PHYSIOLOGY. *Volume 7. Edited by Lawrence R. Blinks; associate editors, Leonard Machlis and John G. Torrey. Annual Reviews, Palo Alto.* viii + 456 pp.; ill. 1956.

Volume 7 of the *Annual Review of Plant Physiology* contains 17 articles, out of the twenty originally announced as in preparation. There seems to be a trend toward a larger number of articles per volume of the *Annual Review;* twenty-five titles are stated to be in preparation for the next issue. The present volume includes articles on: Mineral Nutrition of Plants (E. Epstein), Energy Transformations in Photosynthesis (L. N. M. Duysens), Nitrogen Fixation by Photosynthetic Organisms (G. E. Fogg), Endogenous Rhythms in Plants (E. Bünning), Physiology of Cell Division (H. Stern), Obligate Parasitism (C. E. Yarwood), Biological Relations of Plant Viruses (C. W. Bennett), Iron Chlorosis (J. C. Brown), Photoperiodism in Woody Plants (P. F. Wareing), Plant Proteins (C. E. Danielson), Physiology of Root Elongation (J. G. Torrey), Mechanisms of Carbohydrate Breakdown in Plants (B. Axelrod and H. Beevers), Physiology of Seed Germination (E. H. Toole, S. B. Hendricks, H. A. Borthwick, and V. K. Toole), Phosphorus Metabolism and Photosynthesis (D. I. Arnon), Absorption and Translocation of Plant Regulators (J. Van Overbeek), Effect of Light Quality on Plant Growth (E. C. Wassink and J. A. J. Stolwijk), and Recent Advances in Plant Physiology in the U.S.S.R. (A. L. Kursanov).

The review by Bünning on endogenous rhythms is of considerable interest, in great part because most of the literature on this subject is in German. For various reasons, the concept of endogenous rhythms in plants has been treated with great scepticism by many American plant physiologists. From reading the review article, however, it becomes evident that the concept has undergone fairly recent modifications, so that most of the phenomena that Bünning and others have studied might now just as easily be called, say, "Damping Oscillations in Plant Reactions." With this modification, there should be much less resistance to the interpretations of the German workers, and amazingly enough it now appears that all along they were working with the same or similar plants, and on the same or similar reactions, as their American or British colleagues.

For the most part the present set of reviews continues in the pattern of previous volumes in attempting to present some fairly coherent, over-all concept or set of concepts as a framework for discussion of the articles reviewed. This is not true of the article on plant physiology in the U.S.S.R., written by Kursanov, which is not much more than an extended bibliography. However, there are 400 references to this bibliography, and it will be a great help for any physiologist who is interested in finding out whether anything has been done at all in his specialty in the U.S.S.R. in recent years.

The article on obligate parasites is, almost by definition, a review of negative results; for once an organism can be grown successfully in culture, it can no longer be included as an obligate parasite. In spite of this handicap, Yarwood has prepared an interesting compilation of partial successes, and has looked into the various possible correlations among organisms that refuse to grow in culture.

As is well known to plant physiologists, D. I. Arnon and coworkers have recently discovered a system, using isolated chloroplasts, that can change light energy into phosphate-bond chemical energy. The original papers by Arnon were subject to extreme criticism by workers in photosynthesis, because of his failure to give due credit to previous advances in the field, and for giving the impression that Arnon's discovery was the first, as well as the latest, word on the subject. The review by Arnon in this volume of *Annual Reviews* would appear to be an effort to set the record straight in this respect. Actually, in my opinion, it goes too far in the direction of giving credit to his predecessors. It has become evident, since the first announcements of photosynthetic phosphorylation in vitro, that this does indeed represent the most important step forward in recent years, in the analysis of the biochemistry of energy relationships in photosynthesis. The review article gives so much space and attention to preliminary, indirect evidence for phosphorylation that it almost fails to put the discovery of the in-vitro system into proper perspective.

Among the other reviews, that by Epstein on mineral nutrition summarizes evidence for an interesting modification of the usual concept of ion transport. Although ion transport can still be an active process, it now appears that a major part of the volume of a root can take in ions by passive diffusion. Furthermore, it appears quite likely that most of the ions reaching the top of the plant from the roots have arrived by a pathway involving only this "apparent free space," without the need for successive active transport through each of the living cells along the way.

The biochemical aspects of plant physiology are represented in four articles in this issue: the two on photosynthesis, the article on proteins by Danielson, and the article on carbohydrate metabolism by Axelrod and Beevers. The proteins referred to are the bulk proteins found in seeds. The advances in carbohydrate metabolism discussed by Axelrod and Beevers have been very striking ones; however, just as striking is the very small amount of space needed to describe recent advances in our understanding of the mechanisms for forming polysaccharides.

A. T. JAGENDORF

THE CHEMISTRY AND MODE OF ACTION OF PLANT GROWTH SUBSTANCES. *Proceedings of a Symposium held at Wye College (University of London) July, 1955. Edited by R. L. Wain and F. Wightman. Academic*

Press, New York; Butterworths Scientific Publications, London. $9.50. xii + 312 pp.; ill. 1956.

This book contains the 26 papers of a symposium organized around the following topics: Natural Auxins, Chemical Structure and Biological Activity, Metabolism and Mode of Action, and Applications of Kinetics to Auxin-Induced Growth. The contributors, from Austria, Germany, Holland, Norway, Sweden, Great Britain, and the United States, are outstanding workers in the field, and the papers presented are of a high caliber.

While it is not possible to mention each paper, one aspect of the symposium was noteworthy. Most of the early work in this field suffered because of the lack of a good quantitative method of assaying for plant growth substances. It was evident that there were several biologically active growth hormones in plants, but it was not possible to separate and identify these substances. New methods are presented in several papers in this symposium, largely based on techniques of paper chromatography, which should greatly facilitate studies in the distribution and metabolism of plant growth substances. These new techniques will materially advance our knowledge of the fundamental action of plant growth substances.

The papers are research reports, not review articles, and will be of interest to all botanists who wish to keep abreast of the latest developments in the rapidly expanding field of plant growth substances.

G. R. NOGGLE

PHOTOSYNTHESIS. *Methuen's Monographs on Biochemical Subjects.*

By Robert Hill and C. P. Whittingham. John Wiley & Sons, New York; Methuen & Company, London. $2.00. viii + 165 pp.; ill. 1955.

This excellent and authoritative monograph should undoubtedly prove to be a very important and welcome addition to the literature on photosynthesis. In keeping with the principle of the Methuen monograph series, the authors have succeeded admirably in presenting the present-day knowledge of photosynthesis in a brief but lucid manner. In spite of its brevity, a great wealth of material is available in this volume. All of the more important aspects of the biochemistry and physiology of photosynthesis are discussed both from the technical and historical standpoints. Furthermore, the fashion in which the material is presented is such that this volume should appeal to the interested student as well as the research worker in the field. The value of this volume for anyone engaged in research in photosynthesis is beyond question.

ANTHONY SAN PIETRO

ECONOMIC BOTANY

THE COMPLETE BOOK OF GREENHOUSE GARDENING. *By Henry T. and Rebecca T. Northen. The Ronald Press Company, New York.* $6.50. x + 353 pp. + 66 pl.; text ill. 1956.

The authors of this book are practicing biologists and gardeners, and they appear to know whereof they speak. Writing for the home gardener rather than for the commercial grower, they deal most thoroughly with the practical aspects of growing plants under glass: selecting, building, and managing a greenhouse, the ways of growing healthy plants, and the plants most successfully handled. Not everyone today can own a greenhouse, but for those who can, this book provides a storehouse of sound information. For those who cannot afford the luxury of an expanse of glass, the book is valuable for the gardening hints which can be applied to the growing of house plants in general. Numerous illustrations and a readable text make this a desirable volume for a library shelf.

C. P. SWANSON

LEHRBUCH DER PHARMAKOGNOSIE FÜR HOCHSCHULEN. *Eighth Edition.*

By George Karsten; revised by Ulrich Weber, assisted by F. Oehlkers and E. Stahl. Gustav Fischer Verlag, Stuttgart. DM 36.80. viii + 422 pp.; ill. 1956.

The new, revised edition of this textbook follows the same general organization as the previous editions (1st ed., 1903), and, although chemical constituents are listed and indications of uses given, the emphasis is entirely on vegetable drug anatomy. The drugs are classified in a morphological system. As a textbook of microscopy of whole-plant drugs, the treatise is unsurpassed in its accuracy and relevancy and as such must be highly recommended. The book contains more than 600 illustrations, partly in color, and mostly histological. Both from a didactic and an artistic standpoint they evoke admiration.

During the last 20 to 30 years, a continual change of emphasis has been occurring in the teaching of pharmacognosy. Morphological and histological treatment of drugs of biological origin has been reduced, to the benefit of a consideration of the chemical, biochemical, and physiological aspects of natural drugs. The conspicuous advances which have taken place during the last generation in biochemistry and in the fields of hormone study, vitamin study, and immunology are left unconsidered in this textbook, while, on the other hand, a large number of crude drugs are discussed which are used very seldom, if at all, by physicians today. For this reason, the book conveys somewhat the impression of being out of date. Evidently, the need for the in-

clusion of more modern aspects of pharmacognosy is also felt by the authors, for they state that they plan to "undertake the preparation of another, truly revised edition."

EGIL RAMSTAD

ANALYSIS OF SOILS AND PLANTS FOR FORESTERS AND HORTICULTURISTS. (*Diagnosis of Soil Productivity by Field and Laboratory Methods*).

By S. A. Wilde and G. K. Voigt. J. W. Edwards, Ann Arbor. $3.75. x + 117 pp.; ill. 1955.

The material in this book should be of interest to a considerable number of biologists who have occasion to measure soil fertility and productivity levels. Most soil-testing services are geared to evaluate soil samples in terms of fertility levels necessary to support field crops. However, horticulturists, nurserymen, foresters, ecologists, and conservationists need to collect soil data of a different sort. It is to this group that the book is addressed. The book contains field and laboratory methods for analyzing the physical and chemical properties of soil and ground water, for determining the microbiological population in soil, humus, and composts, and for analyzing plant tissue. In addition, methods are given for the floristic and mensurational analyses of native vegetation cover, as well as methods for the determination of the morphological and physiological characteristics of nursery stock. The methods and procedures are well described and a reasonable amount of information is given on the interpretation of results.

G. R. NOGGLE

GENERAL AND SYSTEMATIC ZOOLOGY

THE INVERTEBRATES: *Echinodermata, the Coelomate Bilateria. Volume IV. McGraw-Hill Publications in the Zoological Sciences.*

By Libbie Henrietta Hyman. McGraw-Hill Book Company, New York, Toronto, and London. $10.00. viii + 763 pp.; ill. 1955.

In the continuation of this fine work on the invertebrates, the Echinodermata have been dealt with more comprehensively than ever before. Among the landmarks in the literature of this phylum are the works of Bather in Lankester's *A Treatise on Zoology* (1900) and of L. Cuénot in the *Traité de Zoologie* (1948). The former dealt exhaustively with fossil forms; in the second, the emphasis is upon anatomy and embryology. In the present work the author has dealt as briefly as possible with the extinct forms but has contributed a wealth of original drawings: the book is especially valuable for its inclusion of sections on physiology, ecology, and behavior, and for its excellent accounts of the geographical distribution of each class.

The classification subdivides the phylum into the Pelmatozoa, of which all but some Crinoidea are extinct, and the Eleutherozoa, comprising the remaining four classes with living forms, together with a small class of wholly extinct echinoderms, the Ophiocistioidea. The arrangement follows the general pattern of previous volumes in this series and concludes with a discussion of phylogeny which is limited to an account of evolution within the group. Consideration of the relationships with other phyla is deferred until these have been described in succeeding volumes.

The elucidation of this phylum was without doubt an immense task. It has been accomplished with the vigor and authority characteristic of the author.

ANNE HUDSON

A CATALOGUE OF THE AMERICAN HESPERIIDAE, *indicating the classification and nomenclature adopted in the British Museum (Natural History). Part IV (Groups H to P) Hesperiinae and Megathyminae. By Brigadier W. H. Evans. The British Museum (Natural History), London.* £4 1s. vi + 499 pp. + 35 pl. 1955.

This volume completes the publication by Brigadier Evans on the specimens of New World Skippers in the British Museum. A previous work covered those of the Old World. During the preparation of this part, some 31,000 specimens were studied. These are arranged in 184 genera (of which 54 are described as new), 1024 species (213 new), and 330 additional subspecies (153 new). In addition, the names of 728 species and 53 genera are placed in synonymy. Of the names regarded as valid, the British Museum collection includes the types of 415 species and 198 additional subspecies; and of the synonymized names, 100. In two appendices are given a list of names wrongly assigned to the New World and a considerable number of addenda and corrigenda to Parts I–III.

As pointed out in reviews of the previous parts (*Q.R.B.*, 27: 402, 29: 171 and 267. 1952, 1954), this monumental work will set the standards for years, perhaps for generations, to come in the classification of this group. It is highly unfortunate, however, that the author was unable to make use of the extremely large collections of the New World museums, especially those of the American Museum of Natural History and the United States National Museum. While not proportionately as rich in types, these collections contain material of a great many of the names which, lacking or inadequately represented in the British Museum, have here been placed in synonymy. Much of this work will, therefore, have to be redone. The time is past when major revisional work can be based on a single collection, even the peerless one of the British Museum. Nevertheless, although laboring under extreme difficulties, Evans has brought to completion a mono-

graphic work of major status that is without parallel or equal in this large and important group of the Lepidopterea.

ALEXANDER B. KLOTS

THE TYPE MATERIAL IN THE J. B. SMITH AND G. D. HULST COLLECTIONS OF LEPIDOPTERA IN THE AMERICAN MUSEUM OF NATURAL HISTORY. *Bull. Amer. Mus. nat. Hist., Vol. 106, Art. 2.*

By Frederick H. Rindge. American Museum of Natural History, New York. $1.00 (paper). Pp. 91–172. 1955.

A LABORATORY AND FIELD MANUAL OF ORNITHOLOGY. *Third Edition, Revised.*

By Olin Sewall Pettingill, Jr. Burgess Publishing Company, Minneapolis. $5.00. xii + 379 pp. + 1 chart; text ill. 1956.

This standard manual has now evolved to the stage of a textbook, since its size has been increased by 100 pages and a good index has been provided. Some chapters (e.g., on territory and mating) are taken unchanged from the 1946 edition (*Q.R.B.*, 21: 385. 1946), while others (e.g., on migration and song) introduce wholly new material and organization. The author has most commendably sought advice from users of his previous editions and has incorporated their suggestions for improvement. The new chart and explanation of the role of weather in migration are excellent, and the increased emphasis on physiology is noteworthy. The manual, however, is definitely elementary and ornithological. Many other ornithological aspects, especially the ecological ones, are mentioned very briefly. The author in many cases (for example, through census methods) correctly avoids the complications of an advanced treatment. The book can now be used not only by students as a manual but as a reference work as well.

DAVID E. DAVIS

BIOLOGY OF THE LABORATORY MOUSE.

By The Staff of The Roscoe B. Jackson Memorial Laboratory; edited by George D. Snell; 7 contributors. Dover Publications, New York. $6.00. xii + 407 pp.; ill. 1956.

This is an unabridged and unaltered reprint of the first edition (*Q.R.B.*, 16: 493, 1941.) It is well printed and should continue to serve as an indispensable handbook for all research workers using mice as experimental animals. To those who are geneticists or are engaged in cancer research it is particularly significant.

ECONOMIC ZOOLOGY

HAWKS, OWLS AND WILDLIFE.

By John J. Craighead and Frank C. Craighead, Jr.; frontispiece by Walter A. Weber; drawings by Jean Craighead George; photographs by the authors. The Stackpole Company, Harrisburg; Wildlife Management Institute, Washington. $7.50. xx + 443 pp. + 1 pl.; text ill. 1956.

Research in wildlife management is plagued by many problems. Pressure for practical solutions, need for cooperation of many disciplines, lack of basic principles, and immaturity are a few. The objective of this book is to understand and evaluate the effect of the aggregate population of raptors on the population of prey over a period of time. To accomplish this purpose, the authors accumulated data about numbers of prey (mammals and birds) and predators (hawks and owls) in an area in southern Michigan in 1941–42 and in 1947–48. The text, tables, and figures describe the data in considerable detail and present a wealth of information on the local situation. No attempt will be made here to abstract the data, but merely to comment on the conclusions drawn.

The approach to the problem lacks a theoretical basis, and results in a description of observations. Furthermore, there are practically no statistical tests of significance of differences, so that one cannot judge the effects of sampling. The census techniques for mice, especially in 1941–42, are very crude and thus only gross relationships are discernible. A major theoretical fault is the failure to understand density-dependence. A conclusion which has been stated many times in the last 50 years is (p. 188) that prey are taken in proportion to their abundance. But the real point is the nature of the proportionality at different densities. This aspect is not explored, although there is a hazy discussion of limiting and controlling factors (pp. 184–187 and 336).

The evaluation of predator pressure was made by examination of the food eaten in nature and calibration to amounts eaten in captivity. From this relationship it is concluded that the predators accounted for nearly one quarter of the mouse populations and that "raptor predation must be recognized as an effective biological control." But there is no mention of other causes of death, especially diseases. What is the evidence that these mice would have survived if the predators had not killed them? Without proof that the mice were less abundant with predators than without, it is not permissible to draw the conclusion.

This book illustrates a lack of fundamental principles and of an experimental approach to game management problems. A mass of data is accumulated but remains undigested because principles were not adequately explored.

DAVID E. DAVIS

PHEASANTS IN NORTH AMERICA.

Edited by Durward L. Allen, frontispiece and drawings by Bob Hines. The Stackpole Company, Harrisburg; Wildlife Management Institute, Washington. $7.50. xviii + 490 pp. + 1 pl.; text ill. 1956.

A group of authorities from various parts of North America has written chapters under the able editorship of a recognized specialist in game management. Each chapter describes in general terms the problems and conditions of the region and in a few cases gives original data. The final chapter summarizes prospects for hunting pheasants, but does not describe basic principles or evaluate the data. Persons interested in pheasants will find that this compendium provides information regarding all the habitats, but few relationships are disclosed that permit derivation of principles.

DAVID E. DAVIS

COMPLETE BOOK OF THE WILD TURKEY.

By Roger M. Latham; illustrated by Ned Smith. The Stackpole Company, Harrisburg. $4.95. xx + 265 pp.; ill. 1956.

The turkey hunter will derive pleasure and profit from this excellently prepared book on the biology, management, and hunting of wild turkeys in Pennsylvania. Sound biological principles are described in the first two parts. Difficult issues of management are not avoided but are treated forthrightly, so that the hunter will understand the fundamental reasons behind various procedures. The biologist will appreciate the detailed descriptions of age and sex characteristics. However, the author has purposely omitted the details of data on various aspects, and the biologist will have to wait for the research papers to verify the conclusions stated in the book.

DAVID E. DAVIS

FINCHES.

By Ian Harman; illustrated by R. A. Vowles. All-Pets Books, Fond du Lac. $3.00. vi + 138 pp. + 8 pl.; text ill. 1955.

A chatty, British, but informed manual for finch-keepers, covering a variety of topics: the construction and maintenance of aviaries, bird rooms, cages, and hospital cages; the care of finches, with particular attention to sanitation requirements and exercise; a practical catalog of diseases and remedies; the bandaging and splinting of fractures; how to perform amputations when necessary—"with a pair of sharp scissors"; egg binding; parasites, etc.

A section on foods outlines basic dietary requirements, the nutritional value of common birdseeds, and such common weeds as can be beneficially added to a finch's diet. The major portion of the book is devoted to a listing of those finches, buntings, grosbeaks, weavers, whydahs, waxbills, and mannikins more usually bred as aviary or cage birds. The particular breeding and nesting habits, as well as diet of each bird, are described.

JAMES J. HILL

"THE COW KILLERS" *with the Aftosa Commission in Mexico.*

By Fred Gipson, with drawings by Bill Leftwich. University of Texas Press, Austin. $4.95. x + 130 pp.; ill. 1956.

The "cow killers" are the members of a joint Mexican-American Commission charged with the eradication of the dreaded hoof-and-mouth disease, which gained a foothold in Mexico in the late 1940's. The Commission was a mixture of scientists, cowboys, and Mexican soldiers, and they did their job well in ridding the country of the disease. But during the course of the vaccinations and the slaughtering of diseased animals, the Commission invariably stepped on the toes of the common people who could neither understand the need for the Commission's work nor appreciate the apparent wanton killing of many animals. And these people, used to oppression and skilled in ways of combating it, fought the Commission as best they could, sometimes with comedy, sometimes with tragedy, but always with seriousness.

This is the story of their resistance. In a series of short vignettes, the author and the illustrator tell of the work of the Commission and the reactions of the people. It is a volume subtly and delicately done. There are tears as well as laughter, pathos as well as ribald humor, but throughout there is dignity and sympathy. It is a book well worth the reading.

C. P. SWANSON

ANIMAL GROWTH AND DEVELOPMENT

DEVELOPMENT OF VERTEBRATES.

By Emil Witschi. W. B. Saunders Company, Philadelphia and London. $8.50. xvi + 588 pp.; ill. 1956.

Embryologists who complain, with justice, of the dearth of adequate textbooks of comparative embryology, will wish to subject Witschi's *Development of Vertebrates* to a careful, critical scrutiny in order to evaluate its qualifications for use in college courses in embryology.

The book is divided into seven sections. The first is a short introduction, the second a discussion of the

germ cells. The third is a brief summary of fertilization, cleavage, and gastrulation; the latter process is, however, also more fully treated in the sections dealing with special forms. These follow: the fourth, a long one (118 pages) deals with amphibians; the short fifth section (about 24 pages), with fishes; the sixth section (126 pages), with birds; and the last (179 pages), with mammals.

The sections which will be of most interest to most readers—those on amphibians, birds, and mammals—contain a variety of material ancillary to embryology in the narrowest sense, of a sort not always included in textbooks of embryology written at this level. Over half of the section on amphibians describes larval organogenesis and anatomy, and metamorphosis. Of the section on birds more than one third relates to a study of late fetal (sic) or early posthatching development (we return below to further talk of the fetal bird). More than one third of the section on mammals takes up the membranes and placentation, lactation, and endocrine control of the reproductive functions. Late stages of organogenesis are treated considerably more exhaustively for the frog than for the mammal. Within the confines of the special divisions, too, Witschi has diversified the materials he covers; in the chapters on birds, for instance, the sparrows and red-winged blackbirds contribute many illustrations.

Whether the book is appropriate as a substitute or supplement for already available texts must be decided, however, not on the basis of the choice of material covered, but on the manner of its covering. A number of embryologists will certainly question many of Witschi's individualistic interpretations; to name only a few, his emphasis on the discreteness of the axial rudiment as source of the notochord and floorplate of part of the neural tube, and on the separateness of the angioblastema. His flat statement that the primordia of lungs and bronchi represent a seventh pair of pharyngeal pouches, and his description of the pulmonary arteries and veins as "the afferent and efferent vessels of the seventh aortic arch," while interesting, are not yet universally accepted, to say the least.

In fact, an outstanding feature of the volume is its tendency to take on an authoritarian tone. For example, in discussing the human embryo, where no experimental evidence is available, Witschi says of the rim-mesoderm and the streak-mesoderm that "it seems beyond doubt that the celomic epithelia are produced by the former, the somites by the latter." Can anything seem beyond doubt in human embryology? "Germ and conceptus are the most acceptable terms for general reference to early stages of human development"—most acceptable to whom? He describes his own system of stage-numbering as standard. Does not the word *standard* usually signify something generally accepted or established? Have Witschi's stages yet met the test? He presents drawings of two fate maps of human embryonic discs, with no word in legend or text that the reviewer could find to indicate to the beginning student that these are purely hypothetical and not derived, like the more usual fate maps, from the results of marking experiments. Is this wise pedagogy?

Heterodoxies of interpretation clearly have their place somewhere in the biological literature. In some sense, the expression of heresies is a prime factor in the furtherance of scientific progress; they provide an indispensable stimulus to work which will either upset them or establish them as at least temporarily accepted concepts, until new interpretations supplant them as they may have supplanted the old. Whether or not they are appropriate for inclusion in textbooks for beginning students, especially one couched in such dogmatic terms, is however an open question.

One of Witschi's most extreme heterodoxies is a return to the old orthodoxy of the recapitulation theory. By his inclusion of embryological data in a rigid evolutionary framework he reflects a strong contemporary neo-evolutionary dogmatism, which has influenced him so deeply as to move him to re-stage the commonly used laboratory embryos according to his own personal, or what he considers evolutionary, criteria. Thus he considers the chick to metamorphose between 4½ and 7½ days of incubation, living the rest of its days within the shell as a fetus; the human embryo metamorphoses at between 6 and 8 weeks of gestation.

Although many embryologists, on theoretical grounds, may disagree with these conclusions of Witschi, it is of course his privilege to couch his interpretations in these terms if he so desires, and if he is able to do so without prejudice to established embryological data with which his interpretations might seem to be at variance.

The preparation of lists and descriptions of stages in embryonic development is not only a convenience, but also a stringent necessity to embryological investigators, for reasons too obvious to enumerate. The choice of stages must always seem arbitrary, and in one sense there can be no right or wrong criteria for making the selection. Or to put it in another way, it must be the embryo, and not the investigator, who chooses the stages.

Now it has been one of the basic tenets of embryology since the days of von Baer that each embryo develops according to its own kind. Embryos do things differently than one another, and many embryologists have agreed that the sequence of stages characteristic of one species of embryo is not necessarily appropriate for application to another species. Witschi thus tends to devaluate much observed and recorded embryological data in constructing a scheme in which he seems to consider every stage of one embryonic species to be comparable to a specific stage of another. But much more far-reaching in its danger for the beginning student is the degree to which he has failed to refer adequately to other investigators' criteria for staging. He does present a brief table listing his own stages, in groups, in

comparison with groups of the Harrison and Glaesner salamander stages. So far as the Harrison stages are concerned, he refers for these to a 1937 paper of Detwiler's in which selected stages are considered, but never to the complete list and drawings of these stages published by Hamburger with Harrison's authorization. He does not say, to the best of my knowledge, where the descriptions of the Glaesner stages are to be found. The Hamburger and Hamilton stages of the chick, and Nicholas' stages for the rat listed and described in Nicholas' chapter in *The Rat in Laboratory Investigation*, and Shumway's studies of the frog stages are cited, so far as I could ascertain, neither in text nor bibliography; in fact, their existence seems never to have been so much as mentioned. The introductory remarks to the bibliography, which conclude by stating that "no exhaustive coverage or documentation is attempted," do not suffice to cover this particular deficiency.

While it is unfortunate and will ultimately prove of more than nuisance value that stages of the same embryos used consistently in most embryological research laboratories are designated differently by different workers, there is a far more important issue at stake. Those who are training the embryologists and biologists of the future hold the responsibility common to all scientists of encouraging students to learn to think and to make judgments for themselves, and this implies making readily available to them as much pertinent information as possible. This principle has been violated in Witschi's presentation. One important fact not apparent in Witschi's phylogenetic table is the close resemblance between student and birds. Students became imprinted too if one does not watch out; quickly, readily, and often almost irreversibly. Their early ideas remain often their dominant ones for life. In the light of what has been said above, instructors will do well to guard themselves carefully in assigning Witschi's book, which may turn out to be useful only to the occasional *rara avis*.

JANE OPPENHEIMER

ANIMAL MORPHOLOGY

ANATOMY OF THE HONEY BEE.

By R. E. Snodgrass. Comstock Publishing Associates, a Division of Cornell University Press, Ithaca. $6.00. xvi + 334 pp.; ill. 1956.

Since there now exist four modern books dealing with the behavior and physiology of the honeybee, namely, von Frisch's *The Dancing Bees*, Ribbands' *The Behaviour and Social Life of Honeybees*, Butler's *The World of the Honeybee*, and Khalifman's *Bees*, the time is indeed appropriate for the appearance of a book on the anatomy of the honeybee. Moreover, it is fitting that the task should have been undertaken by Snodgrass. The present volume is not a revision of *The Anatomy and Physiology of the Honeybee*, although many of the drawings from that earlier work have been used. Complete rewriting, new additional illustrations, and attention to all developmental forms of the bee, from egg to adult, mark this new book. It retains the same high quality and excellence which have come to be the hallmark of this author. To all who are interested in the honeybee in particular or in insect anatomy in general, this volume will be indispensable.

V. G. DETHIER

THE HUMAN BODY. *Its Anatomy and Physiology. Third Edition.*

By C. H. Best and N. B. Taylor. Henry Holt & Company, New York. $6.75. xii + 723 pp. + 8 pl.; text ill. 1956.

THE HUMAN ORGANISM.

By Russel Myles De Coursey. McGraw-Hill Book Company, New York, Toronto, and London. $5.75. viii + 550 pp. + 1 pl.; text ill. 1955.

In an increasing number of universities, survey courses in Human Biology have become acceptable as meeting the science requirements of the non-science major. Both Best and Taylor's *The Human Body* (not to be confused with the same authors' *The Living Body*) and De Coursey's *The Human Organism* meet the demand for a textbook for such courses. Both cover the same general territory of human anatomy and physiology. Best and Taylor's book gives the impression of possessing a greater depth of penetration into the intricacies of the human body. However, since De Coursey has managed to bear in mind that the student who will be using this book probably has had only a minimum of science training, *The Human Organism* may well prove to be the more usable of the two. At any rate, De Coursey's book possesses a flavor of genuineness which Best and Taylor's lacks. Both books contain many beautiful anatomical charts which are clearly labeled. This leads to two questions: Does memorization of such labels really have "cultural" value for a freshman non-science student? And does the student subjected to such rigors gain the proper perspective of biology which is, after all, the study of *βιος—life*?

A. KURT WEISS

THE SCIENCE BOOK OF THE HUMAN BODY.

By Edith E. Sproul; illustrated by Kathleen Elgin. Pocket Books, New York. 35 cents (paper). xx + 232 pp. + 32 pl.; text ill. 1955.

This popularized study of human biology is organized

in 15 chapters on a primarily anatomical basis. The illustrations—mostly simple line drawings in black, but some in red and black—are simple to the point of crudeness. But the text is much better than the bargain-counter appearance of the book seems to promise. It is clearly and concisely written with frequent reference to physiology, pathology, etc., in a primarily anatomical account of its subject. It is a book for the layman that can well serve for general education in its subject at an easy and elementary level.

F. N. Low

An Introduction to Human Anatomy. *Fourth Edition.*

By Clyde Marshall; revised by Edgar L. Lazier. W. B. Saunders Company, Philadelphia and London. $4.50. xiv + 420 pp.; ill. 1955.

This small work on human anatomy (third edition, *Q.R.B.*, 21: 296. 1946) is a commendable presentation of its subject at the undergraduate college level. The illustrations, consisting of half-tones and line drawings, are satisfactory, and there is a useful index. The book should also be useful for the training of nurses, physical therapists, etc., but it is too brief to serve as a textbook for medical students.

F. N. Low

Proctologic Anatomy. *Second Edition.*

By R. V. Gorsch. The Williams & Wilkins Company, Baltimore. $8.00. xvi + 310 pp.; ill. 1955.

The first edition of this work was published in 1941 by The Tilghman Company under the title *Perineopelvic Anatomy*. In the present edition the material has been entirely revised, largely rewritten, and brought up to date. The book contains 9 chapters, 5 of which are systematic while the remainder deal with general areas. There is a wide variety of good illustrations, ranging from line drawings to half-tones. Each chapter closes with an extensive bibliography; an adequate index is provided. It is a book designed primarily for the proctologist and the anatomist, and contains little that would be of interest to the general biologist. But it is an excellent monograph that deserves a respected place in the literature dealing with topographical anatomy.

F. N. Low

Le Système de la Vie Végétative. *Anatomie Schématique de l'Appareil Nerveux.*

By René-Marcel de Ribet. G. Doin & Cie., Paris. 2,500 fr. (paper). 487 pp.; ill. 1955.

This systematic and thorough account of the autonomic nervous system is divided into two main parts, the first covering the autonomic centers, both central and peripheral, and the second the autonomic nerves. The text describes the centers, the ganglia, and their nerves with reference to their function, general location, and relationships to each other. Related anatomy receives attention only when necessary to clarify the location of the parts. The entire book is in outline form and is primarily descriptive. It is very detailed and, in general, quite carefully organized. It should make an excellent source book for the pure anatomy of the autonomic nervous system.

F. N. Low

Brain Mechanisms in Diachrome.

By Wendell J. S. Krieg. Brain Books, Evanston. $7.00. xvi + 188 pp. + 2 charts; ill. 1955.

This unusual volume is apparently an expression of the author's conviction, already familiar to those who know his *Functional Neuroanatomy*, that the representation of three-dimensional relationships is essential to the teaching of neuroanatomy. The book is focused upon a series of six thick sagittal sections of the human brain. These are three-dimensionally represented in both medial and lateral aspects and are printed on transparencies in brilliant colors. A second set of uncolored drawings of the rat brain is included. Both are cover inserts separate from the bound portion of the book. The text is written largely around these drawings, and refers frequently to them and to 55 ancillary text figures. The text itself does not attempt a complete neuroanatomical coverage; it omits microscopic appearances (except the cortex), detailed structure of neurons, nerves, and neuroglia, and much detail concerning blood vessels, meninges, and gross anatomical features. It is intended to be used as a supplementary textbook by medical students and as a major textbook by other groups whose requirements are less demanding.

Krieg's unusual presentation of the subject matter apparently stems from certain basic convictions as to proper approach, convictions which will not be shared by all. The three-dimensional approach requires a simultaneous presentation of all structural features of any importance, and nowhere do functional systems come into focus in their entirety. A contrasting method, that of representing neural pathways in functional systems from origin to termination, has been uniformly successful ever since the functional systems themselves were discovered. The absence of any systematic designation for such systems in black-and-white, three-dimensional drawings may have stimulated the use of color in the present volume, since color distinctions are used here for this purpose. But similar hues are used to represent nearby tracts of related (or doubtful) func-

tion, and the various systems still do not appear as clear-cut entities. With regard to the use of color for clarity, it is well to remember that serious investigators of histological structure find themselves eliminating color as much as possible. They do so until a nearly colorless preparation is obtained, as, for example, tissue stained with iron hematoxylin, because structure is then delineated in greatest detail. Similarly, in teaching, color should be used sparingly in the representation of structural detail. An eye-catching profusion of bright colors tends to defeat its own purpose by distracting attention from the basic structures illustrated. The diachrome colors under consideration are too pretty, too bright, and too numerous to achieve a good pedagogical effect. A further limitation of the diachrome set is that the spinal cord is not included, since it is described in a short chapter in the text.

The points cited above are but a few examples of the questionably chosen devices and essentially fragmentary organization of the book. It fails to present a coherent picture of the central nervous system as a whole. As a result, it almost totally lacks clarity, the prime requisite of any textbook.

It is unfortunate to be obliged to level such severe criticism at an effort that has involved such a high order of diligence and skill as must have been required for the preparation of this book. It is praiseworthy in its purpose and new in its approach, but it is my considered opinion that it fails to make a valuable contribution to neuroanatomical literature.

F. N. Low

ANIMAL PHYSIOLOGY

PHYSIOLOGIE DE L'INSECTE. *Second Edition Revised. By Rémy Chauvin. L'Institut National de la Recherche Agronomique, Paris.* 3.500 fr. 917 pp.; ill. 1956.

As Chauvin himself states in the Preface to this, the second edition, the writing of a book on insect physiology now surpasses the powers of any single person. Nevertheless, he has undertaken the task again in order to fill lacunae and correct faults in the first edition of his book. One must consider the enormous effort which lies behind this presentation and admire the courage that prosecution of the task required. The book suffers from those defects that naturally attend an attempt on the part of a single person to gather together such an enormous volume of factual information. In many respects it has the characteristics of a handbook rather than of a synthesis or organized presentation of the physiology of a particular class of animals. On the other hand, it contains a great amount of detail, tabular material, and illustrations which are not available in Wigglesworth's or Roeder's treatises. It is a different kind of book; it possesses real value as a source book.

The subject of insect physiology is expanding so rapidly that all aids to the compilation of data should be welcomed. The differing points of view of various surveyors of the field provide a healthy means of analysis, evaluation, and criticism. Insect physiologists should have this book.

V. G. DETHIER

COLLEGE PHYSIOLOGY.

By Donald M. Pace and Benjamin W. McCashland. Thomas Y. Crowell Company, New York. $5.50. xxiv + 615 pp.; ill. 1955.

The title which was selected for this book does not reveal what is contained in it. While it does contain the material which its authors feel is suitable for a course in college physiology, it might be supposed to be a textbook in general physiology. As it is, the book turns out to be one which deals primarily with the functions of the human body, but which gives that overworked subject matter a new treatment. In the Preface, the authors state that their aim was to prepare a textbook which would "provide the foundation for students whose main interest lies in the various fields of zoology and also for those whose chief concern is with the functions of the human body alone. The zoological approach is everywhere in evidence. . . ."

After brief sections dealing with basic phenomena of living organisms, skeletal structure, and motility, the discussion of organs and organ systems commences with a study of striated muscle. Subsequent parts, each consisting of a number of chapters, are entitled Nervous Coordination, Receptors, The Transport System, Respiration, Nutrition and Elimination, and Endocrine Glands and Reproduction. The unique features are two. Clinical observations are cited only occasionally and then only to illustrate basic physiological principles. Each chapter begins with a brief account of physiological mechanisms in non-vertebrate and vertebrate forms of life; even plant physiology is occasionally included. This book, then, stands in the center of the triangle which has been formed by the general physiology books of Davson, Heilbrunn, and Mitchell, the comparative physiology books by Prosser et al. and by Scheer, and the many "smaller" human physiology books of intermediary difficulty.

While as a whole the book is a good one and a welcome addition to the textbooks which can be considered suitable for undergraduate physiology courses in American colleges and universities, the rather abbreviated treatment which the non-mammalian forms of life have received may be of concern to some. It is frequently possible to introduce basic principles of physiology which have a wide range of application

while studying simple forms of life. It is true, for example, that many of the zoology majors who will use this book have already heard in some detail, and seen in the laboratory, at least some aspects of the manner in which specific protozoa can maintain their water balance. While what is briefly stated in regard to this on one page of the text is worthwhile, one wonders if more could and should not have been said to biology majors at this time, not only about the elimination of metabolic waste products, but also about maintenance of the "milieu intérieur" in general and of the osmotic equilibrium in particular. One wonders also why a short discussion of excretion in invertebrates is immediately followed by a more comprehensive one on excretion in mammals without any mention of non-mammalian vertebrate excretory mechanisms, such as the aglomerular type of kidneys of some fish. Similar comments could be made concerning almost every chapter.

Some minor corrections will undoubtedly be made if a second edition should become necessary. The terms "complemental and supplemental air," for example, have been replaced in the literature by the phrases "inspiratory reserve volume" and "expiratory reserve volume." The former is usually found to be somewhat larger than the latter. Also, is the phrase *calorific* value of food, which the authors use, a more proper term than *caloric* value?

Most of the comments above have been concerned with matters of opinion and are not intended to detract from the positive features of this book, which discusses the basic principles of physiology clearly, is well written and interesting, and presents an original approach to the subject.

A. KURT WEISS

HUMAN PHYSIOLOGY. *Fourth Edition.*

By F. R. Winton and L. E. Bayliss. Little, Brown & Company, Boston. $8.00. xii + 616 pp. + 1 pl.; text ill. 1955.

Physiology is fortunate that the master synthesists Winton and Bayliss have made it their field of labor. In the slightly less than 600 pages of this volume they have compressed the broad, solid basis of fundamental principles upon which specialized forms of human physiology as well as medicine are built. In this they were assisted by some of their outstanding British contemporaries, who were called upon to contribute chapters in those fields in which they have established themselves as leading investigators. Thus, H. Barcroft has written the chapter on circulation, M. de Burgh Daly that on respiration, R. A. Gregory that on digestion, and D. H. Smyth that on metabolism and nutrition. W. H. Newton and O. C. J. Lippold have prepared the chapter on reproduction, D. R. Wilkie that on muscle, and D. Whitteridge those dealing with nerve and the central nervous system; W. Feldberg and Whitteridge combined their efforts for the discussion of transmission at nerve endings, and Feldberg alone is responsible for the brief chapter on the autonomic nervous system. J. A. B. Gray contributed to the chapter on sense organs, in which A. F. Rawdon-Smith and D. B. Fry wrote the section on hearing; G. W. Harris prepared the chapter on the ductless glands. Winton and Bayliss themselves have written only the introductory chapter which is entitled Physiological Activity, the three chapters dealing with blood and blood gas transport, urine, and body fluids, as well as the sections on taste, smell, and vision in the chapter on sense organs. Their contribution, however, is not adequately measured by the number of chapters actually written by them. They have exercised an editorial influence on all participants which apparently was welcomed by those concerned and which has resulted in the production of a book that, unlike certain other multi-author publications, actually represents an integrated whole. Even the layout is noteworthy. The chapters are divided into clearly discernible subchapters; these, in turn, have further subdivisions with pertinent titles printed in heavy type at the beginning of the appropriate paragraph. Key words appearing in the text are often printed in italics; historical and conjectural material, as well as technical descriptions and illustrative problems, are set in smaller type. This arrangement makes scanning the page easy.

The book, however, is not perfect. The discussion on artificial respiration, for example, could be improved. Nonetheless, this book is one of the best in the field of human physiology. Some students may want to pursue certain aspects of a problem in greater detail; others may wish to read up on the clinical applications of the principles under discussion. For these there are many weightier volumes which can be consulted. This book, however, does give a clear, accurate, and concise picture of the topics covered. It can be recommended to students in science, medicine, and allied fields, and ought to be in every biology library. Last but not least, it can be heartily recommended to workers in the various fields of science who wish to become better acquainted with human physiology.

A. KURT WEISS

HUMAN PHYSIOLOGY AND ITS APPLICATIONS.

By Harrison M. Tietz. Burgess Publishing Company, Minneapolis. $4.25 (paper). viii + 224 pp.; ill. 1955.

This is not a laboratory guide, as its format, binding, and title might suggest, but rather a lecture syllabus of a very unusual course given at Pennsylvania State University. Most topics are discussed under the three

headings of anatomy, physiology, and practical considerations. The anatomical considerations are of the most elementary kind; the sections on physiology are incomplete and contain many errors; while under "practical considerations" a great number of diverse topics are brought together for considerations and platitudes. "The ear is a delicate organ," comments the author. It "can be injured by picking out the wax with some blunt object. A good rule is to put nothing in the ear. In this way one will avoid puncturing the drum which will cause deafness."

It must be stated that the drawings are original and the schematic presentation of the chemistry of muscular contraction makes use of a particularly clever set of symbols.

A. KURT WEISS

THE BODY FLUIDS. *Basic Physiology and Practical Therapeutics.*

By J. Russell Elkinton and T. S. Danowski. The Williams & Wilkins Company, Baltimore. $10.00. xxii + 626 pp.; ill. 1955.

This book is directed primarily to clinicians, but illustrates very nicely Claude Bernard's view that "there is no separate science of medicine or physiology, there is only a science of life." During the past three decades, one of the most far-reaching advances in medical science has been the application of laboratory methods to the diagnosis and treatment of sick people. The results of this development have greatly increased our knowledge of disease processes and our ability to deal with them. But it has also resulted in the fact that the physician is faced with an enormous and steadily increasing amount of physiological information which must be evaluated. The present volume summarizes current knowledge in the field of body fluid dynamics. It consists of four sections, beginning with fundamental concepts of biochemistry and physiology pertaining to the body fluids, presented very simply, and continuing to utilize these principles in presentation of common denominators in clinical problems. This is followed by a discussion of specific disease entities, and by a final section on the practicalities of assessing and correcting disorders of body fluids. The style is fluent and lucid, the chapters short and with good summaries; the chapter bibliographies are extensive. In general, the book is thoroughly sound and well balanced, and avoids the sin of over-facile explanations, although it at times espouses views which would not be acceptable to some workers in the field, or which have been amended in important respects since the bibliographies were closed in April, 1955. Such amendments include the work of Mudge on the mode of action of the mercurial diuretics, and studies of the Landis group on hemodynamics in congestive heart failure. The authors share the usual clinical faith in the physiological importance of the adrenal androgens, a faith that has yet to be validated in controlled laboratory studies. The statement that the adrenal cortex hypertrophies on a low sodium diet (p. 144) is not supported by the literature cited and requires some qualification. Minor defects include Fig. 4-1, in which the legend does not entirely coincide with the figure, and a reference to the *polyvalent* nitrate ion (p. 224).

The great clinical importance of suitable management of the body fluids and electrolytes needs no defense. However, as the authors clearly indicate, in many clinical states the body fluid disorders are secondary symptoms of the breakdown or alteration in fundamental function of some organ or process, and our ability to modify the symptomatology still leaves the primary process out of reach.

EVELYN HOWARD

PRINCIPLES OF RENAL PHYSIOLOGY.

By Homer W. Smith. Oxford University Press, New York. $5.00. x + 237 pp. + 2 pl.; text ill. 1956.

This short and lucid survey of the physiology of the kidney is dedicated "to all students for whom the ever-widening horizons and increasing details of medicine make the art of healing more difficult and yet more certain." Its 180 pages of text are most successfully redistilled from the author's 900 pages on *The Kidney*, published in 1951. The result is not a banal summary for beginners, but a model of clear and concise exposition with which every medical student would do well to be familiar. The author displays an unusually good sense of perspective, so that important matters are not blurred by detail, and yet every phrase is meaningful. There are a number of comments on points often obscure or overlooked by students. There are problems at the ends of various sections, with answers in an appendix which also includes notes on methods, and other data; there is a short bibliography "intended to guide the student to a few articles of historical significance in the development of renal physiology, to reviews . . . and to recent articles which present notable advances in particular fields. . . ." It is estimated that some 2000 papers on the kidney have appeared since the author's bibliography for the larger monograph was closed in 1950 with 2300 references.

While most of the text is devoted to matters fairly well established, it is still so easy to get off the highways in renal physiology that Smith spends some of the time on unpaved routes. A particularly delightful example of this was the following: on the question of the action of the corticosteroids on sodium reabsorption—"At the moment the only well established fact

is that sodium reabsorption is subject to influence by one or more adrenal hormones which presumably promote the reabsorptive process. We have no firm knowledge of what the physiologically important hormones are, of the normal rate of their secretion, of the synergistic or antagonistic action of their metabolic products, of the significance of species differences, of possible changes in physiological action in relation to the amount of sodium or water in the body or the activities of other endocrine glands, and no knowledge of the mechanism of their action. . . . As against this statement, we may call the attention of the reader to the fact that approximately 14,598 papers dealing with the adrenal glands are listed in one bibliography covering the years 1951–53, and most of these papers contain some reference to sodium (and water) balance."

EVELYN HOWARD

NEURAL CONTROL OF THE PITUITARY GLAND. *Monogr. Physiol. Soc., No. 3.*

By G. W. Harris. Edward Arnold, London; [Williams & Wilkins Company, Baltimore]. $6.75. x + 298 pp.; ill. 1955.

This monograph is based on a series of lectures given in the course on physiology for Part II of the Natural Science Tripos at Cambridge University. It has been written "for the student who will, within the course of a few years, be standing on his own feet in the research field . . . and for the specialist in other fields who is interested in physiology in general." For these reasons "no attempt has been made to give a complete list of all the literature in this subject, except in isolated instances . . . where the data have seemed to indicate a "negative" conclusion. The attitude has rather been to present the more important literature, and the points of view more likely to be found true in the light of future work—as it seems to the author."

The book succeeds in presenting a thoughtful, critical, and analytical survey of a great deal of work, much of it necessarily rather tentative and incomplete, in a complex and difficult field. It seems as if we may be at the beginning of a period of great advance in the development of an understanding of the interactions between the central nervous system and the endocrines, in which the pituitary is such an essential effector. The work of Harris and associates, here presented, is an important contribution which every thoughtful student of these questions will want to examine. In addition, the survey of the literature, which cuts across conventional classification of subject matter to a considerable extent, is a valuable contribution to a field which had been in need of this kind of synthesis and evaluation.

EVELYN HOWARD

BIOPHYSICS AND GENERAL PHYSIOLOGY

THE MICROPHYSICAL WORLD.

By William Wilson. Philosophical Library, New York. $3.75. viii + 216 pp.; ill. 1954.

This small book should be read by every biologist if only to give him an idea, in simple terms, of what is going on in the physical world at the micro-level of atomic and molecular structure and behavior. It is a sound presentation of the infinitely small: the structure and behavior of atoms, the meaning of spectra, heat and radiations, the quantum theory, and the transmutation of nuclei. The book is concise, informative and eminently readable, and it should assist the biologist if only by giving him an understanding and an appreciation of the physical and chemical techniques and principles with which he constantly approaches his biological problems.

PROCEEDINGS OF THE FIRST INTERNATIONAL PHOTOBIOLOGICAL CONGRESS (*4th International Light Congress*) *Amsterdam, August 23–28, 1954.*

Editorial Committee: P. B. Rottier, M. Sangster, and J. A. J. Stolwijk. H. Veenman & Zonen, Amsterdam. $8.50. 472 pp. + 25 pl.; text ill. 1955.

Biology which makes use of the ionizing radiations received a tremendous impetus from the development and control of atomic energy, and from the vast amount of money made available for research. In fact, so rapid has been its expansion in all countries that it has tended to obscure the development and importance of a companion field of endeavor, namely, that which makes use of the photochemical rather than the ionizing regions of the electromagnetic spectrum. The separation of radiobiology into two categories on the basis of the radiation used is, of course, arbitrary, and is done primarily for convenience; but it does tend to group biologists with similar interests into societies, and to provide meetings for the discussion of the results of research and of the techniques and instruments developed for the use of radiations of particular qualities. The Comité International de Photobiologie, which sponsored this congress, is consequently a fringe society, drawing its members from other more conventional disciplines such as botany, zoology, chemistry, and medicine. Because it can span disciplines, however, it is important, for such diverse biological areas as photoperiodism, photosynthesis, genetics, luminescence, and some aspects of medicine and public health can be so grouped.

The First Photobiological Congress was held in 1954 in Amsterdam, and the present volume is a record of its transactions. All invitation lectures are included, as are the abstracts of contributed papers. As such, it

provides an excellent cross-section of the photochemical research going on at present in Europe and the Americas. A very substantial part of this type of research, and the greater degree of enthusiasm for photobiology, is European. The inaugural address was given by Professor Koningsberger of Utrecht; three symposia were held respectively on photoperiodism, and on the genetic and dermatological aspects of photochemical radiations; and three sections of contributed papers deal with current research in related fields of biology, medicine, and physical chemistry.

PROGRESS IN BIOPHYSICS *and Biophysical Chemistry. Volume 6.*

Edited by J. A. V. Butler. Pergamon Press, London and New York. $9.50. viii + 274 pp.; ill. 1956.

Again this already excellent series has produced a collection of fine reviews on timely topics in biophysics. Roughly speaking, the 7 articles presented here deal with one of two subjects: the nature of the hereditary determinant, or the mechanism of excitation and conduction in nerve, muscle, and sense cells. The single possible exception is Overbeek's article on the Donnan Equilibrium, but certainly this can be regarded as essential background material for electrical studies on nerve and muscle. The article on protamines and nucleoprotamines, by Felix, Fischer, and Krekels, is well-written and appears to cover most of the important features of these proteins. E. J. Ambrose's article on the structure of chromosomes attempts to correlate some of the more recent results on studies of structure within living cells with the physical chemistry of nucleic acids and nucleoproteins. The article is an excellent extension of an earlier treatment of this subject by Davison, Conway, and Butler, in Volume 4 of the same series. In the article on transforming principles, Zamenhof presents a concise review of the history and present status of this important new discovery in biology. In his article on the Donnan Equilibrium, Overbeek gives a sound and complete discussion of the thermodynamics of electrochemical systems. His discussion of the suspension effect is particularly illuminating and should serve as a basis for interpreting the intercellular potentials which are measured with the aid of microelectrodes. The treatment of the biophysics of the neuromuscular junction, by del Castillo and Katz, is a singularly well-written and extensive review of this subject by two active workers in the field. The characteristics of the excitability of living organisms are discussed by Franck in his article on Models for Biological Excitation Processes. Various phenomenological models of excitable systems are described, and the thesis is advanced that excitability is a characteristic of unstable dynamic (steady-state) systems. DeVries' article on the physical aspects of the sense organs attempts to cover taste and smell, the organs of the labyrinth, hearing, and vision; in doing so he has sacrificed depth for breadth. The review reflects almost exclusively the interests of its author and his own associates. Certainly the mechanics of hearing and theories of hearing deserve as much consideration in a review of this sort as does a discussion of the limits which Brownian motion sets upon the threshold of hearing. Nevertheless, the author dismisses the former with but a few references to the work of von Békésy, Huggins, and others, whereas a tedious 9-page discussion of the latter is presented. A single, thorough review of the mechanics of the organs of the labyrinth and the mechanism of hearing, instead of a spotty review of all the sense organs, would have been more valuable from the point of view of the reader.

It is perhaps of interest to take stock of the subjects which have been treated in the first six volumes of this series. In all, 46 articles have been written in six general areas. There have been 4 articles dealing with the first principles of physics or physical chemistry, 10 on physical methods and their principles, 5 on the molecular structure and physical-chemical properties of macromolecules, 9 on the submicroscopic structure of cells and their components, 14 on descriptions of cellular and subcellular phenomena, and 4 on radiation biology. If one considers these articles as representative of biophysics in the large, then this can be said: by and large, biophysicists are interested in understanding the characteristic properties of cells and their components in terms of the laws of matter; they possess an awareness but no major concern over biological problems which arise at higher levels of organizations, i.e., hemodynamics, psychophysics, etc. The situation is similar with regard to biochemistry; while use is made of the accomplishments of the biochemist, the major interests are not directed toward the elucidation of the mechanisms and energetics of the chemical reactions that occur within living cells. In the first volume of this series, the editors said, "excluding biochemistry on the one hand and physiology on the other there lies between a vast and rather amorphous field of study of which the frontiers and lines of demarcation are anything but well defined." While editors Butler and Randall may not have defined this amorphous field of study, there is no doubt that they have succeeded in extracting from it a coherent body of knowledge which is directed toward the understanding of biological phenomena in terms of the concepts of physics, and which is properly called biophysics.

F. D. CARLSON

BIOCHEMISTRY

METHODS OF BIOCHEMICAL ANALYSIS. *Volume III. Edited by David Glick. Interscience Publishers, New York and London.* $9.50. x + 457 pp.; ill. 1956.

Like the previous two volumes (*Q.R.B.*, 30: 309 and 31: 64. 1955, 1956), this addition to the series covers a dozen or so topics in individual chapters. Volume III differs, however, from its predecessors in layout. It has a division of topics into three recognizable groups, within which individual chapters appear to have a loosely planned relationship to each other. Balance has been maintained between the inclusion of older techniques with modern improvements, and the newer methods still undergoing considerable refinement. In the choice of authors, Glick has apparently followed a policy of establishing this series on the broadest possible base, and in some cases where two topics could have been equally well presented by the same author, they have in fact been assigned to two. Thus a maximum of viewpoints is represented.

Volume III contains chapters on organic phosphorus, lipoic acid, and histamine analyses. Also included are the enzymatic micro-determinations of uric acid, hypoxanthine, xanthine, adenine, and xanthopterine by using ultraviolet spectrophotometry. Carbohydrate chemistry is represented by 3 chapters, respectively on periodate oxidation, on group analyses of polysaccharides, and on the use of infrared analysis for the determination of carbohydrate structure. Metals and trace metals are considered in 5 chapters, with respect to their own determination, their relation and interaction with other molecules, and their use in techniques involving other substances. Specifically these chapters deal with complex ion stability as measured with ion exchange resins, analysis of metal-protein complexes, the use of metal buffers and indicators, and the application of flame photometry and spectrometry to trace metal analysis. Of these, the methods for the determination of zinc in biological material are presented in a separate chapter.

As a part of the whole series, *Methods of Biochemical Analysis, Volume III* is highly recommended.

CLAUDE F. BAXTER

ORGANIC CHEMISTRY, *with Special Reference to its Significance for the Biological Sciences. Revised Edition. By Robin Charles Burrell. Burgess Publishing Company, Minneapolis.* $4.25 (paper). x + 243 pp.; ill. 1955.

Professor Burrell has stated his objectives clearly and in detail in the Preface and the introductory chapter to his book (first edition, *Q.R.B.*, 24: 380. 1949). "So if you don't want understanding along with information, it would be to your advantage to repair immediately to sources of the information you want and not waste your time on a four year curriculum in Agriculture." Adhering to this viewpoint throughout, he has presented the serious student with a mature and thoughtful approach to an understanding of the key position which organic chemistry plays in biological processes. The book is packed with lore which must continuously whet the interest and appetite of the student who wants to know. Admittedly, its complete mastery in a semester would constitute a fair feat of memory, yet the book will certainly serve as a valuable reference work which the graduate may wish to utilize after all his examinations are finished. For this reason, one might wish that the book had appeared in a more permanent format.

The task of compressing into a one-term course the ideas and information needed by a practitioner of the complex chemical arts associated with plant or animal physiology, bacteriology, or nutrition must always seem hopeless of realization to the teacher who wishes to avoid "force-feeding" and "indigestion" on the part of his charges. Burrell's approach is to choose from the rich store of substances whose application to the problems of physiology and growth is immediately obvious. Fundamental principles underlying this superstructure should seem more meaningful to the student really interested in these matters; thus an economic and professional impetus is provided to stimulate the effort required for mastery of the subject.

ALSOPH H. CORWIN

CHEMICAL PROPERTIES OF ORGANIC COMPOUNDS. *An Introduction. By Elliot N. Marvell and Albert V. Logan. John Wiley & Sons, New York; Chapman & Hall, London.* $4.75. x + 326 pp.; ill. 1955.

While it is not explicitly stated, it may be presumed that this textbook is intended for the type of specialized short course in organic chemistry presented to students of nursing and home economics and to similar students who need more chemistry but would prefer to take less. For such an audience, the text seems to move at an appropriately easy pace and not to attempt more than can be assimilated reasonably in one semester. Students who have mastered this textbook will, however, gain little of the flavor of organic chemistry as a science, which proceeds from experimental observations to conclusions and generalizations. They will, instead, have a series of descriptions and modern dogmas, some small percentage of which may at some future time possess utilitarian value, if recalled from the limbo of hastily crammed materials studied in preparation for the inevitable examinations.

The major portion of the text is relatively free from serious errors. Unfortunately, the closing chapter on proteins has half a dozen errors and vacillates between the correct dipolar ion formulations for amino acids and the erroneous uncharged formulations. Technically, the book is of good quality and shows skilled craftsmanship throughout.

ALSOPH H. CORWIN

FORTSCHRITTE DER CHEMIE ORGANISCHER NATURSTOFFE. *Volume XIII.*

Edited by L. Zechmeister. Springer-Verlag, Wien. $25.60 (cloth); $24.75 (paper). xii + 624 pp.; ill. 1956.

This volume, like its predecessors, contains a series of extremely valuable articles. In the first of these, A. R. H. Cole describes the methods of infrared spectral analysis, their theoretical bases, and their application, particularly to steroids. The chemistry of the gallotannins and of the tanning derivatives of ellagic acid is discussed by O. Th. Schmidt, who also develops an interesting hypothesis on the biosynthesis of these substances. Ch. Tamm describes the properties and the structure of the cardiac glycosides; his article ends with a Table in which the melting points, optical activities, ultraviolet absorption spectra and lethal doses of 200 of these glycosides are listed. Natural tropolones and their derivatives are treated in an excellent chapter written by T. Nozoe. It may be surprising to many of us that this interesting group of 7-membered cycloheptatrienes comprises biologically interesting substances of a great variety, such as colchicine, purpurogallin (occurring in the galls of oak leaves and formed in vitro by the oxidation of pyrogallol), and stipitatic or puberulic acid, which is found in certain molds. It is also interesting that cycloheptatriene was first prepared by the degradation of alkaloids of the atropine group which contain the saturated 7-membered ring. In the following chapter, J. R. Price reviews the alkaloids with quinoline, acridine, furoquinoline, and quinazoline structure, excluding the Cinchona alkaloids. The increasing use of Rauwolfia alkaloids as hypotensive and tranquillizing agents made it necessary to supplement the last survey of them given in Vol. X of this series. A. Chatterjee and S. C. Pakrashi report on the alkaloids of *Rauwolfia canescens* and *R. serpentina*, particularly on yohimbine, reserpine, serpentine, ajmaline, and alstonine. The pharmacological action of these new drugs is discussed by G. Werner. In the final chapter, W. Grassmann and E. Wünsch give an authoritative review of the methods of peptide synthesis and of the underlying reaction mechanisms. Most of these articles clarify in an admirable manner complicated fields of research, show to many of us that there is systematic order where we may not have seen it before, and thereby give new and interesting vistas into the ever-increasing world of organic natural products.

FELIX HAUROWITZ

FIBROUS PROTEINS AND THEIR BIOLOGICAL SIGNIFICANCE. *Symp. Soc. exp. Biol., No. IX.*

Academic Press, New York. $8.00. viii + 370 pp. + 40 pl.; text ill. 1955.

This volume contains the papers which were presented at a Symposium of the Society for Experimental Biology at Leeds, England, in 1954. While considerable time has elapsed since the symposium was held, this book, like previous editions of the same series, is an outstanding and valuable contribution.

An introductory review of the field is presented by W. T. Astbury, followed by a discussion of the basic chemistry of proteins by F. Singer. A consideration of deoxypentose nucleoproteins, as an example of a fibrous structure, is presented by E. Chargaff. Various experts in the field adequately demonstrate the biological importance of collagen in chapters on the distribution and metabolism of collagen, the influence of collagen on the organization of apatite crystallites in bone, and fibrinogenesis of connective and skeletal tissues in the embryonic fowl. The medical implications of this subject are briefly discussed in a chapter on collagen diseases.

Several chapters are devoted to the physical characteristics of collagen. These include: configuration of collagen and gelatin molecules in condensed and dispersed states, x-ray diffraction studies of collagen fibres, observations on native and precipitated collagen, and states of aggregation of collagen.

Five chapters are devoted to extensive discussions of skeletal muscle, including proteins of the myofibril, components of the myofibril and their relation to structure and function, the structural basis of contraction in striated muscle, and some observations on the infrared spectrum of muscle. The final contributions to the volume involve fibrous proteins from numerous sources such as bacterial flagella, cilia, the mitotic apparatus, and the nucleus.

This is an advanced treatise. It is certain that all active workers in the area will find the volume a useful addition to their libraries.

ROBERT VAN REEN

THE CHEMISTRY AND REACTIVITY OF COLLAGEN.

By K. H. Gustavson. Academic Press, New York. $8.00. x + 342 pp.; ill. 1956.

As a major constituent of skin, tendon, bones, and

connective tissue, collagen is one of the most widely distributed proteins of the animal kingdom. For that reason, this compilation is likely to find widespread acceptance. The volume, which is intended for both the expert and the non-specialist reader, competently covers various basic aspects of the chemistry and properties of collagen.

The first chapter gives a brief discussion of protein chemistry, with emphasis on end-group analysis, internal structure, and some special properties of proteins. Next, the author discusses the structure of skin and makes the intriguing observation that the different degrees of hydrothermal stability of the skin collagens of cold-water and warm-water fishes and land mammals are correlated with the hydroxyproline content of the skins. In discussing the architecture of collagen, x-ray, electron microscopic, and birefringence findings are all explored. In subsequent chapters, the isoelectric points, effect of alkali, and reversible and irreversible reactions are presented. Further topics are the hydration of collagen, swelling, the effect of electrolytes and nonelectrolytes, and the thermal shrinkage of the protein.

A chapter on the inactivation of specific groups of collagen will be particularly useful to those who are interested in mechanisms of action and in studies of the general reactivity of collagen. A brief mention is made of unhairing, the removal of epidermal matter, and the conversion of collagen into gelatin.

In this treatise, the author is most interested in the collagen obtained from hides and skins. No mention is made of the collagen of bones and little is said about other collagenous tissues. The medical researcher, however, might find the volume of value in view of its emphasis on chemistry rather than on applications of skin collagen.

ROBERT VAN REEN

BLOOD GROUP SUBSTANCES. *Their Chemistry and Immunochemistry.*

By Elvin A. Kabat. Academic Press, New York. $8.00. x + 330 pp.; ill. 1956.

For many years the study of immunochemistry has been the examination of reactions between two chemically undefined reactants to form a product whose nature was even more obscure. The growth of this science has been gaining momentum for the past fifty years until the immunochemist is now on the verge of dealing with reacting species of antigens and antibodies whose chemical structure is known. The contributions which have led to so satisfactory a situation have now been reported and critically evaluated for the cases of the blood group substances by E. A. Kabat.

For the reviewer this book was an introduction to some aspects of immunochemistry; and consequently the detail which was devoted to reporting experimental findings impeded rapid assimilation of the main points. On the other hand, this extensive coverage of original data would probably be of great aid to the investigator whose interests have led him into closely associated fields. The author unfailingly made clear the main points, either before or after considering the detailed evidence. He also was careful to present a statement of the principles involved and the type of information available for a given hypothesis. For this reason the book can be read profitably by novice as well as immunochemist.

The first two chapters contain a historical introduction to the study of blood group substances and a review of the principles of immunochemical procedures. Next the variety of sources of blood group substances is presented; such unusual origins as the gastric mucosa, saliva, urine, commercial peptones, spermatozoa, and leucocytes are intriguing. Some plants contain antibody to blood group substances, but to what purpose is not known.

Succeeding chapters do not form distinct divisions of the topics suggested by their titles but are extensively dovetailed. The purification of blood group substances from different sources is discussed, many methods are considered, and certain ones are selected and recommended on the basis of the author's experience. The similarities of blood group A, B, O(H), and Le^a substances from different animals are discussed from the standpoint of chemical composition: four sugars occur in all preparations, namely, D-galactose, L-fucose, D-glucosamine, and D-galactosamine. Polypeptide substances are also present. The basis of analysis depends on the purity of the preparation; hence one chapter is devoted to criteria for purity and another to chemical composition and properties. An additional area is explored by the chapter on the immunochemical similarities and differences among blood group substances from various species.

Many attacks have been made on the structure and properties of blood group substances. One chapter reports the effects of various chemical and enzymatic agents. Following mild acid hydrolysis, carbohydrate fragments are removed and additional specific reactive sites appear. Sodium carbonate hydrolysis also splits off carbohydrate. An enzyme that attacks hog A substance but not hog O is discussed. Similarities between human A and O erythrocytes were revealed by an enzyme that converts the former into the latter. Additional structural information was obtained by studying the inhibition by simple sugars of the action of enzymes on blood group substances.

The book is concluded by two chapters: Antibodies to Blood Group Substances and their Biological Effects, and Biological Effects and Uses of Blood Group Substances. Included here is an evaluation of a thermodynamic study of anti-A and anti-B reactions with their antigens and a discussion of the relationship of blood group substances with various biological charac-

teristics, such as intrinsic factor, virulence-enhancing factors, and virus inhibitors.

The author frequently points out the future experiments that are needed and presents constructive criticism of the work already done. This attitude makes the book worthwhile to both the reader of general interests and the specialist.

BRUCE K. JACOBSON

MICROBIOLOGY

GRUNDRISS DER MIKROBIOLOGIE. *Third Edition.*

By August Rippel-Baldes. Springer Verlag, Berlin, Göttingen, and Heidelberg. DM 45. vi + 418 pp.; ill. 1955.

This book (second edition, *Q.R.B.*, 28: 93. 1953) presents an introduction to microbiology from a fairly advanced point of view for students with a good background in chemistry and other basic sciences. Both bacteria and other microorganisms receive comprehensive treatment. The book is well organized and well printed. No obvious errors of fact or interpretation were noted. Abundant references given as footnotes bring the subject well up to date. This textbook continues the tradition of solid, scholarly work for which the Germans were noted before World War I. At the same time, it offers little which is not available in similar textbooks in English. Accordingly, it will be of interest chiefly to those American microbiologists who wish to improve their reading-knowledge of German by using the book as a textbook in a course or for individual reading.

WALTER C. TOBIE

PARASITOLOGY

A HANDBOOK FOR THE IDENTIFICATION OF INSECTS OF MEDICAL IMPORTANCE. *Third Edition.*

By John Smart; with chapters on Fleas by Karl Jordan, and on Arachnids by R. J. Whitlick. British Museum (Natural History), London. 2 £. xii + 303 pp. + 13 pl.; text ill. 1956.

This edition is a photolithic reprint of the second edition (*Q.R.B.*, 24: 54. 1949) with corrections and additions to the chapter on mosquitoes by P. F. Mattingly. There are, in addition, some general additions and corrections. Those readers who have used earlier editions need no introduction to this one. New readers who are interested in insects of medical importance will find this handbook extremely useful. It is authoritative, concise, and profusely illustrated.

V. G. DETHIER

THE NATURAL HISTORY OF TSETSE FLIES. *An Account of the Biology of the Genus Glossina (Diptera). London School of Hygiene and Tropical Medicine, Memoir No. 10.*

By Patrick A. Buxton. H. K. Lewis, London. £4 4s. xviii + 816 pp. + 47 pl.; text ill. 1955.

Insect-borne disease remains a major threat to health over vast regions of the earth in spite of recent spectacular advances in the field of insect control. While malaria at present constitutes by far the most serious insect-borne disease, it will be remembered that sleeping sickness as recently as fifty years ago was killing an estimated 40,000 Ugandans per year and was causing immense financial losses as untended farm lands were reclaimed by the forest and innumerable cattle died of the disease. From this high-water mark sleeping sickness has been forced into its present relatively quiescent status by a sustained attack upon its insect vector. No investigator has been more well qualified to chronicle this unending campaign than Patrick A. Buxton, and we must consider ourselves fortunate that he was able to complete this splendid monograph before his death.

These more than fifty years of concentration upon tsetse fly eradication by a myriad of entomologists have, besides producing salubrious effects on the health of the African and his herds, made the tsetse fly nearly as well known as *Drosophila* in terms of our understanding of its ecology and population dynamics. The physiology of these insects has also become reasonably well known. These matters, together with systematics, morphology, control measures, and the relation of tsetse flies to disease, are covered in great detail in Professor Buxton's monograph, the completeness of which is attested by its more than 600 literature citations.

JAMES F. CASE

HEALTH AND DISEASE

ASCITES TUMORS AS TOOLS IN QUANTITATIVE ONCOLOGY. *Ann. N. Y. Acad. Sci., Vol. 63, Art. 5.*

Edited by Roy Waldo Miner; consulting editor, Theodore S. Hauschka; 54 authors. New York Academy of Sciences, New York. $4.50 (paper). Pp. 637–1030; ill. 1956.

The early work of Loewenthal, Jahn, and Klein has opened up an entirely new approach to cancerous growth since the free cells of the ascites tumor may be handled by techniques which are essentially bacteriological in nature. This has permitted a quantitative approach to problems which are genetic, biochemical, and metabolic, and which could not be studied nearly so well in solid tumors. The 29 papers included in this symposium issue indicate the diversity of the attack

being made on malignant growth, for they deal with aspects of growth, population analysis, cytology, cytochemistry, immunology, radiation biology, chemotherapy, and metabolism. The ascites cell clearly provides oncology with a living system capable of refined study much in the way that Lederberg's study of genetic recombination in bacteria has led to the development of a kind of genetics unknown or unapproachable in higher organisms. It is not feasible to consider each contribution in this review, and it need only be pointed out that the symposium as a whole provides an up-to-date commentary on the status of a very active field of biological and medical research.

C.P. SWANSON

BREAST CANCER, *and Its Diagnosis and Treatment.*

By Edward F. Lewison. The Williams & Wilkins Company, Baltimore. $15.00. xii + 478 pp. + 10 pl.; text ill. 1955.

It is a great pleasure to review this splendid book of Edward Lewison, of the Tumor Clinic of the Johns Hopkins Hospital. The author's style is fluent, free, and delightfully descriptive. The large number of patients with benign and malignant breast disease seen in the clinic has made possible a valuable study of many facets of the problem of breast cancer. The experience with these patients has been utilized to advantage in this volume. Collaborators, including Richard S. Handley, have been wisely chosen because of their special skills in some particular phase of the breast cancer problem. These contributors add authority to the book.

Chapter I, on the history of breast cancer and its treatment, is fascinating as it traces the course of events from primitive and ancient times to the work of Halsted and Willy Meyer in America. The following chapters lay a broad foundation for the study of cancer of the breast: Surgical Anatomy, Physiology of the Breast, Experimental Aspects of Mammary Cancer in Mice, Pathology of Cancer of the Breast, and The Relationship between Benign Breast Disease and Cancer. An important and rather new chapter is one on The Psychological Aspects of Breast Disease.

The diagnosis, biopsy, and various forms of therapy, surgery, and radiotherapy, and the effects of hormone administration are ably discussed. The relation of breast cancer to pregnancy or lactation is an ever-present one and is thoroughly treated in this book. Factors influencing prognosis are evaluated in a chapter devoted entirely to that subject.

An array of statistics, charts, and graphs summarizes a mass of valuable information. This volume is a noteworthy addition to American and world literature of breast cancer, and brings the reader up to date on the latest—although in some instances controversial—methods of treatment. The medical profession is fortunate to have so much practical information in one volume.

GRANT E. WARD

PHARMACOPOEA INTERNATIONALIS. *First Edition. Volume II.*

World Health Organization, Geneva. $6.75. xx + 350 pp.; ill. 1955.

The urgent publication of Volume I of the *Pharmacopoea Internationalis* in 1951 led to the omission from that volume of certain drugs that have very recently come into medical practice. Volume II deals with these pharmaceutical products and a number of dosage forms of drugs included in Volume I. Mention should be made that recognition by the International Pharmacopoea constitutes only a recommendation for a drug, and is not intended to be a legal certification. The endeavor merits support, however, for it may promote a unified code of nomenclature for drugs on a world-wide basis, a measure that is sadly lacking at the present time. Those outside the medical field will be interested in the international cooperative character of the work as described in the Preface to these two volumes.

C. JELLEFF CARR

PSYCHOLOGY AND ANIMAL BEHAVIOR

AN INTRODUCTION TO PSYCHOLOGY.

By Harry W. Karn and Joseph Weitz. John Wiley & Sons, New York; Chapman & Hall, London. $3.90. xii + 315 pp.; ill. 1955.

PSYCHOLOGY. *The Fundamentals of Human Adjustment. Third Edition.*

By Norman L. Munn. Houghton Mifflin Company, Boston. $5.75. xvi + 542 pp. + 6 pl.; text ill. 1956.

PSYCHOLOGY.

By Delos D. Wickens and Donald R. Meyer. The Dryden Press, New York. $5.25. x + 541 pp. + 2 pl.; text ill. 1955.

These three books on introductory psychology, one of which is the almost completely rewritten third edition of the well-established textbook by Munn, are all intended to serve for a one-term course. Although, following a custom in recent textbook announcements, they all state that the presentation of the subject matter is student-oriented, they differ in the degree and means by which this goal is realized through selection and organization of material.

Karn and Weitz, believing "that an understanding of the facts and principles of psychology can equip the student to learn to deal effectively with many of his own personal adjustment problems," attempt to achieve this purpose by orienting all topics toward the concept of adjustment, that is, "the organism's state of equilibrium in relation to its surroundings." The book is designed for a terminal course for non-majors. Munn's reorganization of the content puts the discussion of individual differences and intelligence at the beginning as topics of personal interest to the student. Wickens and Meyer, by drawing continually on the student's experiences and observations to demonstrate psychological principles, expect that "many of the student's problems of personal adjustment suddenly reappear in a firm context of psychological theory."

The difference in purpose determines the different emphasis on various topics. In Karn and Weitz's book, the biological aspects of behavior are mentioned only in passing and the discussion of the neural and sensory processes is inadequate. Munn has simplified his chapter on the neural foundations of behavior and has made it clear and comprehensive. The two chapters on vision and on hearing and the other senses have been retained. In Wickens and Meyer's distinction between the molar and the molecular levels of behavior, the latter is treated extensively in four chapters dealing wth the body and its parts, sensory mechanisms, response mechanisms, and associative mechanisms.

The books differ equally as greatly in the extent to which they discuss cultural and social influences on behavior. Wickens and Meyer have a separate chapter dealing with the concepts of class, group and role, the psychological mechanisms involved in suggestiblity and conformity, and particularly with the development and measurement of attitudes and opinions. Munn discusses these questions adequately in connection with motivation, personality, and perception. It is surprising that Karn and Weitz, with their life-oriented approach, mention attitude and prejudice only as factors in perception and do not deal at all with the relationships of individuals within the group.

Otherwise, the topics included in these three books are those found in most standard textbooks, except for the fact that Karn and Weitz have no systematic treatment of motivation, but believe that the importance and all-pervasiveness of motivation can best be brought to the student by introducing and discussing it within the context of other related topics. In keeping with their student-orientation, they include a chapter on such persistent adjustment problems in college students as inferiority feelings, nervousness, the control of sex urges, study efficiency, and the selection of a vocation.

All three books will give the student a good understanding of the scientific method used in psychology in so far as the collection of data is concerned. In regard to the evaluation of data, Karn and Weitz include a section on elementary statistical concepts and procedures in their chapter on individual differences. Munn's treatment of this topic is now divided into a discussion of the basic concepts needed for the evaluation of individual and group differences and examples of procedures for obtaining these measures, in the appendix. The omission of statistical methods in Wickens and Meyer's text is justified by the authors in the belief that it is expecting too much of the beginning student for him to be able to evaluate data, and that experimental data can be presented in ways other than by conventional statistics.

In regard to general make-up, the Wickens and Meyer book is far superior to most of the current textbooks in the field. The use of black and red delineates the key areas in representational drawings and points up the data in tables and graphs for better understanding of their significance. Photographs are well selected to show pertinent features of apparatus or experimental situations.

As aids for teaching and studying, both Munn and Wickens and Meyer are accompanied by an instructor's manual and a student's handbook containing not only objective and discussion questions but also descriptions of simple experiments for class demonstration and for the student's use. Karn and Weitz add a section of discussion questions after each chapter and provide a book of objective questions for the instructor.

ANNELIES A. ROSE

CHILD PSYCHOLOGY AND DEVELOPMENT. *Second Edition.*

By Louis P. Thorpe. The Ronald Press Company, New York. $6.00. v + 709 pp.; ill. 1955.

This book covers the development of the child from prenatal life to the end of adolescence. As one might expect from the interest of the author, who is professor of education and psychology, the presentation emphasizes the development of the child in regard to educational goals rather than the psychological problems of developmental stages as such. Since each topic is introduced by a discussion of its general concepts and theories, very little background in general psychology is required of the student.

A large amount of factual material is presented in tables, graphs, and schematic diagrams, often more than can be utilized in the text and integrated into the picture of the "whole child"—as the author promises in the Introduction.

The organization of topics is the conventional one starting with the hereditary dispositions and prenatal influences, and treating various aspects of the child's development such as physical growth and health, motor abilities, mental abilities and intelligence, language and thought, children's play and interests, emotional

factors, personality and character formation, parent-child relationships, social education, and mental hygiene. Three new chapters have been added in the present edition. The one on psychosexual development is factual and sensible. In the chapter on School and the Learning Process, learning theories and learning processes at all developmental levels are discussed in addition to the objectives and administration of the modern school, but very little is said about the psychological problems involved in the school situation. The chapter on the characteristics of exceptional children is mainly concerned with the physically handicapped child.

ANNELIES A. ROSE

SIGNS, LANGUAGE, AND BEHAVIOR.

By Charles Morris. George Braziller, New York. $3.75. xiv + 365 pp. 1955.

This is a reprint of a text originally published in 1946, and constituting the major statement by an important modern American semanticist of a theory of signs. It is a pretentious book—the jacket blurb is virtually able to duplicate the author's own statement—and one to be evaluated accordingly.

Morris has attempted to formulate a theory (not a "science") of semantics, ostensibly predicated on certain studies in human and (particularly) animal behavior. His thesis is also predicated on certain aspects of C. S. Peirce's pragmatic theory of meaning, or signification. Unfortunately, however, the author pursues an ambiguity as regards his discipline. His initial statement is that ". . . a science of signs can be most profitably developed on a biological basis." The phrase "science of signs" appears frequently throughout this book; semiotic (semantics) is defined as the *science* of signs. Nevertheless, the author pursues his subject by a logical and verbal analysis predicated on preconceived value systems, and utilizes data drawn from biology and psychology to give an aura of "science" to his thesis. His is a methodology which is neither fish nor fowl; it is characterized neither by the rigor of empirical demonstration nor the sharpness of philosophical analysis. As a substitute, the author has constructed a dialectic of jargon, which pervades nearly every page. The glossary does not really remedy the situation: e.g.,

"Locatum. . . . . A significatum of an identifior." (sic)

"Precise sign . . . Signs, not vague, are precise."

The glossary, however, is not the only clue to the character of this book. Although some of the more important historical figures who have exerted profound influences on the development of semantics are mentioned in a very short appendix, The History of Semiotic, the bibliography excludes and indeed the whole book fails to give any adequate consideration to the historical aspects of the philosophy of signs. The author's familiarity with many of the classical thinkers in the field seems to be derived chiefly from secondary sources.

Morris' starting point is the present inadequacy of semantics as a science: "There are few general principles [of semantics] now available in terms of which existing knowledge can be integrated and from which empirically verifiable predictions can be made." To resolve this dilemma, Morris proposes that "every sign involves behavior, for a sign must have an interpretant, and an interpretant is a disposition to a response" (p. 187). Language and all other signs become for Morris solely behavioristic phenomena, and he is consequently able to make such surprising generalizations as the following: "culture is, largely a sign configuration. . . ." (p. 207). Morris makes explicit that he has *equated* the import or significance of every sign with the behavioral response elicited by it. Further than this, he has to one degree or another, and sometimes wholly, equated the problem of semantics with the problems of law, morality, cosmology, logic, et alia. It is clear also that for Morris, semantics has become *the* supreme discipline, and hence has the duty of fixing the limits and relationships of all other disciplines. Altogether this is a most radical and presumptive book, based perhaps fundamentally on a confusion of the tool (language) with the things the toolmaker does with it.

JAMES J. HILL

HUMAN BIOLOGY

MAN AND THE WINDS.

By E. Aubert De La Rue; translated by Madge E. Thompson. Philosophical Library, New York. $6.00. 206 pp. + 16 pl. 1955.

Unless it causes spectacular damage or discomfort, the wind is a factor in the environment which the average man takes for granted. Even the most casual interest and observation will reveal, however, that winds play a much greater role in human activity than is realized. The author has gathered together from personal observation and from the studies of others information concerning the types and names of winds, wind as a determining factor of climate, physiological effects of wind, how to adapt dwellings to wind, the wind as a transporting agent, soil erosion by wind, wind as a source of energy, sailing ships, wind and aviation, mythology and legend, and myriads of other facts. This is a treatment of wind from the point of view of human geography. It might be considered an introduction to the subject rather than a comprehensive treatise. In any case, it makes fascinating reading. Its weakness lies in the fact that its accuracy and detail diminishes with distance from Europe. Some of the minor errors of

fact have been corrected by the translator and are appended as footnotes. It remains a pleasant, informative book.

V. G. DETHIER

THE LOST VILLAGES OF ENGLAND.

By Maurice Beresford. Philosophical Library, New York. $10.00. 445 pp. + 16 pl. + 1 folded map; text ill. 1954.

This is an account of the disappearance, or survival in only two or three dilapidated buildings, of English villages. The theme recalls Oliver Goldsmith's *The Deserted Village* in the land where wealth accumulates and men decay. It also recalls and elaborates the thesis of The Blessed Sir Thomas More in his *Utopia*, that the displacement of agriculture by pasturage of sheep, for the sake of their wool, wrought great harm to country folk (from the fourteenth century to the latter part of the sixteenth century, and reaching the acme of depopulation in the period between 1440 and 1520). As More deplored: "The sheep that were wont to be so meek and tame and so small eaters now, as I hear say, be become so great devourers and so wild that they eat up and swallow down the very men themselves. They consume, destroy and devour whole fields, houses and cities. One shepherd or herdsman is enough to eat up that ground with cattle to the occupying whereof about husbandry many hands were requisite. Look in what parts of the realm doth grow the finest and therefore dearest wool, there noblemen and gentlemen: yea, and certain Abbots . . . leave no ground for tillage, they pluck down towns and leave nothing standing but only the church to be made a sheep-cote." At Calceby, Lincolnshire, the Parson who died in 1621 left "cheeses three times as valuable as his books."

This study by the Lecturer in Economic History in the University of Leeds is a masterly survey of the evidence bearing on the disappearance of villages in England during those centuries, lucidly and entertainingly told. It is a highly special study; and for those interested in the social and political reverberations of technological change—for this was virtually an industrial revolution—the book is treasure trove.

WILSON D. WALLIS

SCIENCE AND ECONOMIC DEVELOPMENT: *New Patterns of Living.*

By Richard L. Meier. Technology Press, Massachusetts Institute of Technology. John Wiley & Sons, New York. $6.00. xviii + 266 pp. + 1 map; text ill. 1956.

The concept of world development is so complex that no specialist can comprehend the interaction of the basic factors, but the author, a chemist and a student of economic and social science, is well equipped for the task and has done an excellent job.

The present world predicament is first pictured in relation to human needs, world resources, and population growth. The demographic data on population growth, based upon 1950 estimates, are much too conservative, while the view of agricultural resources, based upon Salter's estimates, and of forestry resources, based upon Glesinger's estimates, is probably too optimistic.

The discussion of the science and economic development of new food sources is excellent. It includes not only yeast and algae, but also the possibilities of direct extraction of proteins from the leaves of grasses and legumes. The author is realistic in his awareness that adequate diets will produce larger people, who will then require 20–25 per cent more food. He is not as realistic in his estimates that new food resources might provide a good diet for 50 billion people.

At the *present* rate of growth, a world population of 50 billions would be reached in little more than 200 years. The author recognizes this problem and realizes that population growth could absorb any possible increase in food and energy production. He recommends control of population growth by birth control and more research on physiological contraceptives adapted to the needs of the people of under-developed areas. The author states that any program for economic development rests upon the premise that population growth can be controlled by low birth rates.

The present and future sources of fuel and energy include fossil fuel, atomic and solar energy, and other sources. For most of the world these new sources must be developed soon.

The greatest contribution of this book is its consideration of the development of new patterns of living. The maintenance of the minimum adequate standard of living is estimated to cost about $330 per capita per year and a capital investment of $1800 to $3500. But even under favorable conditions it would require an estimated 50 to 80 years to raise living standards from subsistence levels to adequate ones. The author also considers the social problems of the future in a densely populated and industrialized world, and deals with these with some degree of optimism.

This book presents an excellent survey of all phases of world development, and should be required reading for all who are interested in the economic and social future of mankind.

KARL SAX

TOMORROW'S FOOD. *Revised and enlarged edition.*

By James Rorty and N. Philip Norman. The Devin-Adair Company, New York. $3.95. xii + 297 pp. 1956.

Most of this book (first edition, *Q.R.B.*, 25: 244. 1950) is devoted to the "perverted food habits" of the

American people. According to the authors, our refined and processed foods from crops grown on depleted soils are largely responsible for a host of diseases ranging from arthritis to rickets, and for tooth decay, insanity, and juvenile delinquency. They advocate the use of fresh and unrefined foods grown under a system of "biodynamic" agriculture and uncontaminated by modern insecticides. They are, however, advocates of liberal diets and state that "a daily energy quota of 3500 calories was judged sufficient, and the estimate still stands"! For underweight persons, "additional meals of fruit and milk, say at 10:30 A.M., 4:30 P.M., and at bedtime are permissible."

KARL SAX

THE CULTURAL HERITAGE OF 20TH CENTURY MAN. *Philomathean Lecture Series, 1955.*

By Elizabeth Flower, Alexander Ringer, Pincus Schub, Henry Steele Commager, Morse Peckham, Wallace Davies, Conway Zirkle, Julius Wishner, and Grant Manson. Pennsylvania Literary Review, Philadelphia; The Philomathean Society. 50 cents (paper). 96 pp. 1956.

The nine essays in this volume make up the 1955 Philomathean Lecture Series given at the University of Pennsylvania for the university and the community surrounding it. The first three deal with the integration of Western culture; the fourth, by Henry Steele Commager, is entitled Nationalism and the Great Community of Learning; and the remainder treat the subject of modern man and his nineteenth-century heritage. Only one essay is concerned with biology in particular, that of Conway Zirkle called Darwin's Impact on Modern Thought, in which he discusses modern evolutionary theory and its implications in terms of today's society, and makes clear that it is virtually impossible to stand still in an evolutionary sense. Since this is as true for the human race as for any other biological entity, it would be nice to be able to predict where we are heading. This, however, is a problem to which no answer is at present available.

C. P. SWANSON

INDUSTRIAL SOCIETY. *The Emergence of the Human Problems of Automation.*

By Georges Friedmann; edited and with an introduction by Harold L. Sheppard. The Free Press, Glencoe. $6.00. 436 pp. 1955.

This is a translation of the author's *Problèmes Humains du Machinisme Industriel*, which was published in 1947. Although a few additional notes and more recent references have been added, the text is essentially that of the earlier work. The book contains 18 chapters divided into three main sections. Part One, called The 'Human Factor,' is concerned with the physiology of work, fatigue, the working environment, adapting machines to man, and accidents. Part Two, curiously labeled The Limits of the 'Human Factor,' is generally concerned with problems of automation: monotony, rhythm, assembly-line work, and the changes in occupational skill and training caused by automation. Part Three, Towards a Social Psychology of the Factory, is essentially concerned with the human-relations aspects of modern industry.

To the American reader the chief value of Friedmann's book is that it provides some insight into European philosophy about modern industrialization. The term "rationalization," often found in continental discussions but unheard of in this country, is at the core of this philosophy. A second value of this book is that it cites European literature and draws upon examples from continental industries which the American reader is not likely to have heard of. In other respects, the book is disappointing because most of the work cited is so old. American industry and industrial research have progressed so rapidly in the last fifteen years that what the author has to say seems a little archaic.

A. CHAPANIS

COUNSELING IN MEDICAL GENETICS.

By Sheldon C. Reed. W. B. Saunders Company, Philadelphia and London. $4.00. viii + 267 pp. 1955.

Counseling in Medical Genetics is a compact little volume designed especially for physicians, the natural heredity counselors for the family. With his wide experience in heredity counseling, the author has admirably accomplished his intent in preparing a practical book. Detailed information is limited to human abnormalities occurring as frequently as once in a thousand persons. A chapter is devoted to each of the following: mongolism; spina bifida (together with anencephaly and hydrocephaly); clubfoot; harelip and cleft palate; congenital heart diseases of various types; mental retardation; general body build; pyloric stenosis; congenital dislocation of the hip; fibrocystic disease of the pancreas; blood genetics; skin color; convulsive seizures; susceptibility to rheumatic fever and tuberculosis; allergies; and schizophrenia and manic-depressive psychosis. Using these fairly common pathological conditions, the author acquaints the reader with the most complicated types of human inheritance and the methods by which the geneticist evaluates various risks of the appearance of abnormalities among sibs.

Obviously the greatest benefit of heredity counseling lies in allaying unfounded fears or in acquainting people with the probabilities of their having to accept the economic and emotional distress of an afflicted child, should they, with a given hereditary background, decide on further reproduction. The philosophy of heredity counseling insists that parents alone should

make decisions as to having children once the counsel has been given. Specific examples of requests made at the Dwight Institute and replies given appear at the end of each chapter. From these examples the emotional benefit of heredity counseling to the client is obvious.

This book is highly recommended to all physicians, medical students, and teachers of medical students. A list of heredity clinics in the United States and Canada is included for physicians who wish to refer cases for counseling. For those interested in details not included in the scope of this volume there is an extensive bibliography. A second printing of this excellent book should, in my own opinion, include a chapter on the genetic bases of cancer.

SARAH B. PIPKIN

BIOMETRY

STATISTICAL METHODS, *Applied to Experiments in Agriculture and Biology. Fifth Edition.*

By George W. Snedecor; Chapter 17, on Sampling, by William G. Cochran. The Iowa State College Press, Ames. $7.50. xiv + 534 pp.; ill. 1956.

This, the fifth edition of Snedecor's highly useful and successful book, should be even more popular than its predecessors. Among the technical changes made in this version are the introduction of a few of the newer nonparametric statistics which are so useful in dealing with biological data, the alteration of some of the notation and terminology to make it more consistent with current usage, a reorganization of the material on factorial experiments, a more explicit discussion of the models of the analysis of variance and the way in which the model affects the significance test, and a chapter on sampling by one of the world's experts on the topic, William G. Cochran.

Snedecor's style of writing continues to be generally free and easy. It is refreshing to find an author who is not afraid to use the personal pronoun "I" and to address the reader with a direct "you." I think more textbook writers should follow suit.

A. CHAPANIS

DE OMNIBUS REBUS ET QUIBUSDAM ALIIS

A PRACTICAL MANUAL OF MEDICAL AND BIOLOGICAL STAINING TECHNIQUES. *Second Edition.*

By Edward Gurr. Interscience Publishers, New York and London. $6.25. xxv + 451 pp. 1956.

Those whose research work requires the mastering of staining techniques are probably familiar with Gurr's *Manual*. The first edition was a model of clarity, uncluttered with theoretical considerations of fixation or staining; the second edition is an improvement within the same limits. Errors have been corrected, new techniques have been inserted, and a new section of histochemical methods has been added. The appendices, in particular, are most useful, including as they do conversion tables, formulae for fixatives and stains, refractive indices of many substances, saturated solutions of reagents in terms of grams/liter, and stain solubilities. The only recent and useful technique which I could not find included is the dry-ice method for making slides permanent; certainly that method would be worthy of inclusion in any practical manual devoted to techniques.

Lacking theoretical considerations, the volume remains nothing more than a grouping of cook-book methods for doing specific biological jobs. However, the recipes have been tested, and the book is one to keep within arm's reach in the laboratory.

C. P. SWANSON

A SCIENTIFIC SAMPLER.

By Raymond Stevens, Howard F. Hamacher, and Alan A. Smith. D. Van Nostrand Company, Princeton. $6.00. xviii + 413 pp. + 1 pl. 1956.

The *Industrial Bulletin* is a publication of Arthur D. Little, Inc., and for the past thirty years it has provided a running series of "reports, predictions and reflections" in the area of applied science. It reflects, of course, the interests of this particular industrial concern and its staff, but it has also provided a mirror to reveal what is going on in the scientific world at large. The best of these articles, most of which are no more than two pages long, are grouped together into the present volume to provide a fair amount of readable and informative scientific matter for both scientist and layman. The articles are generally grouped into two large sections: The Men, and The Methods; but within each group they are further subdivided to give uniformity and consistency of subject matter. Many of the articles have little reason for being included, having probably once served a purpose, but being no longer of interest or of value. I am tempted to label this a scientific potpourri; it is however, more correctly termed a ragout, but with more beans than meat.

C. P. SWANSON

COAL-MINING.

By I. C. F. Statham. Philosophical Library, New York. $15.00. xii + 564 pp.; ill. 1956.

The biologist will find little in this volume of interest except a single chapter devoted to the origin and occurrence of coal, particular emphasis being given to those sources in the British Isles. The remainder of the book concerns itself with the operation of a colliery and with the industry itself.

THE QUARTERLY REVIEW OF BIOLOGY publishes critical reviews of recent researches in all of the special fields of biological science. The contribution should present a synthesis or digest of the researches and a critical evaluation of them. A mere synopsis of the literature without evaluation or synthesis is not desirable.

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